PROCEEDINGS OF
THE LINNEAN SOCIETY OF LONDON
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250th ANNIVERSARY OF THE BIRTH OF LINNAEUS

Proceedings of the Reception held in the Rooms of the Society on Thursday, 30 May 1957 at 8.0 p.m.

The President, Dr H. Hamshaw Thomas, M.B.E., F.R.S., received the Guests which included His Excellency the Swedish Ambassador in London; Professor Dr Bertil Hanström, F.M.L.S., representing the Royal Swedish Academy of Sciences, Stockholm, and the University, Lund; Officers and members of the Swedish Institute in London, and the Anglo-Swedish Society, representatives of Learned and Scientific Societies, and Universities and Colleges in the United Kingdom and members of the Linnean Society of London.

By courtesy of the President and Council of the Geological Society Addresses were delivered in the Meeting Room of the Geological Society, and were relayed to the Library and Meeting Room of the Linnean Society.

Before the Addresses were delivered, His Excellency the Swedish Ambassador presented to the Society, on behalf of the Swedish Linnean Society, a copy in Silver of the Medal struck by the Swedish Royal Mint to commemorate the 250th Anniversary of the Birth of Linnaeus, and on behalf of the Royal University, Uppsala, a work entitled, *Inbjudningar till Doktors-Promotionerna I Uppsala Universitets Aula fredagen den* 31 *Maj* 1957. Uppsala, 1957.

Professor Dr Bertil Hanström, F.M.L.S., presented to the Society, on behalf of the University of Lund, a copy in Silver of a Medal commemorating the 250th Anniversary of Lund University in 1918.

The President read a telegram received from the Royal University, Uppsala, 'Uppsala University sends its Best Greetings and Thanks the Linnean Society for Good Guardianship of Linnean Inheritance. Segerstedt.'

His Excellency the Swedish Ambassador in London, Mr. Gunnar Häglöf, then delivered an Address entitled ' Sweden in the time of Carl Linnaeus ' **[Printed below]** and Mr W. T. Stearn, F.L.S., delivered an Address entitled ' Botanical Exploration to the Time of Linnaeus '. **[Printed below.]**

The following exhibits, with brief explanations were shown in the Library.

A selection from Linnaeus's Shells, Tortoises and Turtles.

A selection from Linnaeus's Fishes, Linnaeus's cultured pearls, and a Loadstone from his Mineral Collection.

A selection from Linnaeus's Insects, etc.

A selection of the works of Linnaeus showing his annotations.

Some Linnaean relics, etc.

A map illustrating journeys undertaken by Students of Linnaeus. (Prepared by the Zoological Secretary.)

A selection from Linnaeus's Manuscripts.

A selection from Linnaeus's Herbarium.

Some works by other Authors from Linnaeus's Library.

The Evolution of the *Species Plantarum*. (Prepared by Mr W. T. Stearn, F.L.S.)

A series of photographs illustrating the Life and Work of Linnaeus. (Presented to the Society by the Swedish Institute, Stockholm.)

Photographs, Engravings and Biographies of Linnaeus.

The Council was greatly indebted to the Director of the Royal Botanic Gardens, Kew, for providing the decorative plants exhibited throughout the Library, and to Messrs Carters Tested Seeds Ltd for the cut flowers displayed.

Copies of a booklet entitled, *Linnaeus*, by Arvid Hj. Uggla, presented to the Society by the Swedish Institute, Stockholm, were distributed to those attending the Reception.

SWEDEN IN THE TIME OF CARL LINNAEUS

By His Excellency the Swedish Ambassador in London

[Read 30 May 1957]

Two hundred and fifty years ago, in May 1707, Carl Linnaeus was born in Stenbrohult, a small parish in the southernmost part of the province of Småland—a particularly beautiful part of the Swedish countryside with beeches and oaks and meadows full of flowers.

At the time when the curate's wife at Stenbrohult gave birth to her first child in that month of May 1707, the King of Sweden was encamped with his armies at the very centre of Germany. The young Charles XII had forced Denmark to capitulate, he had inflicted a heavy defeat on the assembled Russian armies, and vanquished Poland and dethroned her King. Now he was letting his armies rest in Saxony. The great Duke of Marlborough travelled across the continent to meet King Charles at his headquarters in Altranstädt. In the monumental biography which Sir Winston Churchill has devoted to his ancestor he gives a vivid description of the European situation in the spring of 1707. Sir Winston writes : ' Charles XII was now at his zenith . . . Encamped in the heart of Germany at the head of forty thousand devoted, ruthless, athletic, disciplined Swedish co-adventurers, whom no troops had yet been able to withstand, he became the object of the most earnest anxiety and solicitation from all parts of Central Europe '. The meeting between Charles XII and the Duke of Marlborough in the spring of 1707 was therefore what to-day would be termed a meeting at top level. England was leading the great coalition against France ; Sweden was fighting a lone but so far entirely successful war against Denmark, Poland and Russia.

This Swedish empire, which reached one of its culminating points at the very time of Carl Linnaeus's birth, was one of recent date and rapid creation. After the turmoil of the late Middle-Ages Sweden had—much in the same way as England under the Tudors—found a new national inspiration under the royal house of Vasa. During the 16th and 17th centuries Sweden fought an almost endless series of wars against Denmark, Poland, Russia and the Emperor of Germany. Great military victories made Sweden one of the leading European powers. In 1707 the Swedish realm included, apart from Sweden itself, Finland, the Baltic States, the westernmost part of Russia, where Leningrad now lies, and considerable portions of northern Germany.

Only ten years later—when Carl Linnaeus was at school in the little town of Växjö in southern Sweden—disaster had overtaken the Swedish empire. The army had been frozen to death in Russia, and Sweden was attacked by new enemies, Prussia and Hanover. At last the hero-king himself was killed while leading his newly raised armies into Norway. With him ended Sweden's supremacy as a Great Power. From now on Russia entrenched herself on the

Baltic, and Prussia became a great military force. Thus a new balance of power was created in northern Europe and Sweden became of secondary importance. The army, which had been the mainstay of the country, was reduced. The absolute monarchy of Charles was abolished and the Swedish Parliament acquired a dominating position.

Seldom has a once leading European power undergone a more rapid and profound change. When Carl Linnaeus was born, Sweden was in control of northern Europe. When he was ten years old, the country had lost for ever her position as a Great Power, and when he was in his teens a new period in Swedish history began, a period of parliamentary government and party strife, a period which enthusiastic political reformers hailed as the Age of Liberty, but which harsh critics have called an Age of Decline.

The whole trend of Sweden's history was changed. It could even be said that the history of modern Sweden began with the new development in the 1720's. I hasten to point out that this does not in any way mean that the Sweden we know to-day with its industrial prosperity, world-wide commerce and rationalistic outlook existed as early as the 18th century. Certainly not. Sweden in the time of Linnaeus was a poor, sparsely populated country, where agriculture was the chief means of livelihood and the towns, including Stockholm, were quite small and insignificant in comparison with their English or French counterparts.

What I have in mind is rather that the beginning of the 18th century—the time of Carl Linnaeus's youth—saw a gradual reshaping of Swedish history. The urge to conquer new territories, the warlike spirit, the sound of drums and of steadily marching troops, vanish. Instead, the Swedish mind begins to concentrate on what is useful, on what is economical, and on what is rational. The new-born Linnaeus received the name of Carl after the hero-king Charles XII, but in the course of his long and industrious life he became almost a symbol of the new era in Sweden and this in contrast to the previous period, which had been one of military glory and foreign conquests.

It is, of course, true that one should not overemphasize the differences between one period of history and another. The changes which seem so overwhelming in the eyes of an historian looking back a few hundred years, were perhaps hardly perceptible to the contemporaries who lived their lives from day to day.

In the case of Sweden at the time of Carl Linnaeus it is moreover quite clear that some of the institutions and features, which formed essential parts of the Swedish life in the 16th and 17th centuries, retained a great deal of their importance in the new era of the 18th century.

After the Reformation and during the religious struggles of the 16th century, the Protestant Church had become a vital part of life for the entire Swedish people. It was a strong and fighting church greatly inspired by the prophets and the kings of the Old Testament. Their God was not a mild and forgiving one, but a God of strength and of vengeance. The Swedish protestants bore a great resemblance to the more moderate amongst the English Puritans. It is interesting that this stern Old-Testament conception of God and the universe could form the background to an intense appreciation of the beauty of nature—nature as the creation of God. Just as Milton in his *Paradise Lost* can suddenly burst forth in the highest poetry inspired by the greatness and the beauty of nature, in the same way the Swedish religious poets of the 17th century could indulge in the delights of the summer, the forests and the flowers against the stern background of their Old-Testament conception of the world. How well I remember from my own schooldays that beautiful hymn

Oh bless the yearly harvest
and water, Lord, our land,

a hymn written in the 17th century and much loved by Swedish children even in the days of the young Linnaeus. It was this kind of Protestant religion, which was the basis of Linnaeus's whole conception of the world. He, the son of the curate at Stenbrohult, the grandson and greatgrandson of Protestant clergymen, had been educated with a view to entering the Church himself. Even if at a relatively early age he turned his attention from theology to the natural sciences, he retained to the end of his life the basic ideas of this Protestant faith. His God was the stern God of the Old Testament, the creator of nature in all its forms.

Beside the Protestant religion there was another factor of fundamental importance to the Sweden of bygone centuries, which retained its influence in the time of Linnaeus. The Swedish people have always had a strong belief in the virtues of good legislation and methodical and efficient administration. I wonder if this legalistic and administrative instinct is not more pronounced in Sweden than in any other country. As early as in the age of the Vikings the old chronicler Adam of Bremen speaks of the Swedes as governed by the sacred laws of their country. The Swedish Empire of Gustavus Adolphus and Charles XII depended not only on the strength of the Swedish armies but also on the Swedish legislation and administration which were traditionally good. There was no change in these traditions when Sweden lost its position as a Great Power. Rather the opposite. In the first half of the 18th century great new efforts were made both in the codification of Swedish law and in the consolidation of Swedish administration.

It seems to me that the works of Carl Linnaeus bear the imprint of these Swedish traditions. Linnaeus was looking for the laws governing the different provinces of nature. He was very conscious of his task of bringing order into the natural sciences. It is tempting to say that Linnaeus acted as if he felt himself to be the Director-General of the administration of God's own nature. And in this as in so many other respects he followed longstanding Swedish traditions.

The new era in Swedish history, which began in the 1720's, was marked, above all, by the increasing power of the Swedish parliament, and by the growth of different political parties. In fact, the decades from the 1730's onwards were periods of the most intense strife between the two leading political parties, the Hats and the Caps, a strife, which ended only by a coup d'état in 1772, when the young King Gustavus III took command.

It does not appear that Linnaeus took any part or showed even the slightest interest in these political developments, which otherwise dominated the daily life of the Swedish people.

In another respect, however, Linnaeus was more representative of his age. In the course of the 18th century and partly under English influence utilitarian ideas became more and more prevalent. The science of political economy was born. Swedish State Departments began to make plans for new manufacturing industries. The Swedish parliament decided to investigate the national resources of the country. It was for this purpose that Linnaeus was sent out on his journeys to different provinces of the realm. His reports from these tours are written with such vigour, such power of observation, and in so delightful a language that they may be considered his finest literary achievements. But these literary qualities must not make us forget that his books on the Swedish provinces were meant to be reports on the results of his investigations of the natural resources of his country. In short, they were a utilitarian effort quite in keeping with the new ideas of the century.

In Sweden as in England the 18th century brought milder manners, more agreeable forms of social intercourse, greater freedom and—on the whole—better taste in architecture and furniture. The stiffness and pomposity of the

His Majesty The King of Sweden looking through some Linnaean Manuscripts during his visit to the Society on 17 April, 1957

Caroline period gave way to the ease and elegance of the so-called Swedish rococo. The Swedish language became lighter and more pliable.

The personality of Linnaeus was quite in harmony with the spirit and atmosphere of this 18th century. His native language is a delight to read—it has a freshness and a vitality which have hardly ever been equalled. Where could one find a more attractive or more characteristic scene from the 18th century than this contemporary description of one of Linnaeus's botanical excursions round Uppsala with his pupils :—

> ' They were undertaken in a certain order and were made to eight places near the town. At this time he had not less than two to three hundred who accompanied him, all clad in light linen garments, and bearing all necessary devices for the collecting of herbs and insects . . . During each excursion, certain resting-places were ordained, where the scattered students would assemble, and where lessons would be given on their most important findings. When the young men had thus disported themselves in the country from morning to night, they were marshalled for the return march and, with their teacher at their head, the young men trooped to the house in the Botanical Gardens, where a repeated shout of Vivat Linnaeus wound up the pleasures of the day. The mirth, delight and eagerness with which the youths listened to the words of their teacher inspired foreigners, no less than Swedish scholars to share in these pleasures.'

I want to leave with you this vision of Linnaeus surrounded by his pupils in the pursuit of the noble science of botanical research. Linnaeus personified many of the best qualities of his age, and it is not too much to say that Sweden of the middle of the 18th century was the age of Carl Linnaeus.

BOTANICAL EXPLORATION TO THE TIME OF LINNAEUS

By William T. Stearn

[Read 30 May 1957]

When commemorating the birth or death of a great man it is customary to review his achievements. These, however, can rarely be understood properly unless set against the background of his times and the achievements of his predecessors. Moreover, in matters of science, it is important to know what material served as the basis of his work. The 250th anniversary of the birth of Carl Linnaeus (1707–78) provides a fitting occasion to glance at the progress of botanical exploring down to his day, for through this exploration there accumulated that mass of records and specimens which made his life-task of co-ordination and analysis so necessary. Its geographical background has also a practical importance in relation to the type-localities for Linnaean species.

Alone among contemporary botanists Linnaeus worked on a world-wide survey of the plant kingdom. Intellectually, no doubt, that many-sided genius Albrecht von Haller (1708–77) stood on a higher plane but Haller's botanical work was restricted to North Germany and his native Switzerland and he never adopted the binomial system of nomenclature. Hence Linnaeus is honoured in botany the world over and Haller forgotten by all but specialists on the European flora. Linnaeus was, however, neither the first nor the last to tackle this ever-growing task. In 1623 the Swiss botanist Caspar (Gaspard) Bauhin made such a comprehensive botanical review in his *Pinax* ; between 1686 and 1704 the Englishman John Ray did the same, but more elaborately, in his *Historia Plantarum* ; in 1753 and 1754 it was accomplished by Linnaeus in his *Species Plantarum* and *Genera Plantarum* ; between 1801 and 1807 Christian Hendrik

Persoon covered the fungi and flowering plants in his *Synopsis methodica Fungorum* and his *Synopsis Plantarum.* Thereafter the task grew too big to be completed by any one man ; the botanical exploration stimulated by Linnaeus had yielded too much material. In the 19th century Augustin Pyramus de Candolle and George Bentham came nearest to accomplishing for their period what Linnaeus had done for the 18th century. It is of interest to note that in 1874, while hard at work on the *Genera Plantarum* (1862–83 ; cf. Stearn, 1956), Bentham put forward a plan for a new *Species Plantarum.* He accepted Alphonse de Candolle's estimate of the number of species of flowering plants then known as between 110,000 and 120,000, with which may be contrasted Linnaeus's 1753 estimate of the total number of all plants as not likely to exceed 10,000, G. N. Jones's 1951 estimate of known flowering plants as comprising about 250,000 species and J. Angely's 1956 estimate of them as about 380,000 species. Bentham then went on to state that ' a competent botanist would readily get through three or four thousand [short diagnostic descriptions] in a year. In the *Flora Australiensis* I had no difficulty in preparing a thousand to twelve hundred in a year, and that was all original work, entailing the personal examination of every species often in numerous specimens, and a long and tedious investigation of synonyms . . . 300 species a month, with a month or six weeks' vacation, would be no great strain upon the mind.' Here Bentham spoke only for himself, the foremost systematist of his period. Linnaeus when he completed the *Species Plantarum* (1753) had set nearly 6000 species in order and, incredible as it seems, he wrote his final draft covering them all within a year (cf. Stearn, 1957 : 72–73), exhausting himself in so doing.

The idea of this survey of the vegetable kingdom had taken shape in Linnaeus's mind some 20 years earlier, when he was a student at Uppsala, too young and inexperienced to realize fully its extent and difficulties, young enough not to be daunted by what he did know. Thus the years 1732–33, in which Linnaeus both made his journey to Lapland and compiled a first draft of the *Species Plantarum*, can well be taken as ending the pre-Linnaean period of botanical exploration and beginning the modern one, in which Linnaeus's students at first took a conspicuous and significant part (Fig. 1). The present review, necessarily superficial and incomplete on account of the long period and vast area to be surveyed, does not extend beyond 1732.

Although it has been ironically remarked that ' in this country [Britain] we can do botany without botanical names, almost without plants ', botany is not an abstract study. A botanist as distinct from a statistician, nomenclaturist or bibliographer must himself collect plants, either living or dried, for his work, or get others to collect them for him, or make use of those already assembled in herbaria and gardens. Linnaeus did all three. He collected material himself on his Lapland journey of 1732 and on later Swedish journeys ; he stimulated his foreign correspondents to send him specimens and seeds ; his students wandered afar in search of them ; he studied the specimens in the herbaria of Burser, Clifford and others and furthermore he supplemented them by consulting the illustrations in the works of Sloane, Kaempfer, Plukenet, Petiver, Plumier, Commelin and others. As a result his *Species Plantarum* includes species from every continent, except Australia,[1] and from a surprising number of islands. Its scope was limited only by the extent of botanical exploration up to that date.

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[1] The flora of Australia (then called New Holland) was not entirely unknown then. William Dampier (1652–1715) landed in Western Australia in 1699 and brought back to England a few drawings and herbarium specimens from Shark's Bay and the Dampier Archipelago, of which nine were figured in his *Voyage to New Holland* (1703) and six in Plukenet's *Amaltheum botanicum* (on pls. 450–454 ; 1705). These little engravings do not, however, give floral details and would have been of little use to Linnaeus had they come to his attention. Hence Dampier's pioneer work, though historically interesting, contributed nothing of immediate value to botanical exploration. Specimens acquire scientific value by coming into the right hands at the right time. Unfortunately Dampier's specimens now at Oxford (cf. *Proc. Linn. Soc. Lond.*, **159** : 44–50 ; 1939) were unknown to Linnaeus.

Botanical Exploration in General

Botanical exploration presupposes botany, which is organized knowledge about plants, and botany presupposes principles and methods of classification. Knowing names of plants by itself is not botany, but knowing names in such a way that they provide guides to other information, i.e. knowing names which make part of a system of knowledge linking apparently unrelated facts, is essential to botany. Botanical exploration is the business of travelling about an area or region and collecting or otherwise scientifically recording its plants so that they can ultimately be referred to places within such a system. In Linnaeus's time the old systems of classification, of which he gave summaries in his *Classes Plantarum* (1738), were proving inadequate or too complicated for dealing with the varied new material. His own admittedly stop-gap ' sexual system ', although repugnant to the best botanists of the time like Amman and Haller, enabled specimens to be quickly allocated to groups and provided with names instead of going unsorted and unnamed into cupboards. The Linnaean method of botanical recording thus made botanical exploration worth while, for this became a means of contributing on a large scale to the world's knowledge. Therein lies the clue to the zeal for travel that animated so many of Linnaeus's students (cf. Fig. 1).

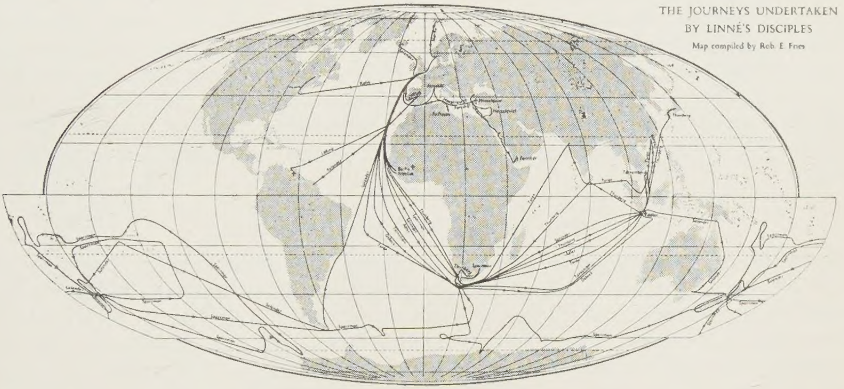

FIG. 1.—The journeys of Linnaeus's students between 1746 and 1796 (after R. E. Fries, 1950)

Botanical exploration, being thus linked to botany as an expanding science, indicates the attainment of a certain cultural level within a community, i.e. that this has become a society in which the acquisition of knowledge about plants as plants has a value of its own apart from economic or medicinal considerations. The pursuit of such knowledge reflects a mental climate still far from world-wide and to many peoples still incomprehensible. They cannot readily believe that sane persons of knowledge and intelligence will expose themselves to hardship and danger and spend money simply to collect useless plants ; unless an alternative innocent explanation less insulting to their own intelligence than that of curiosity can be provided, they see plant collecting as a cloak for guilty or suspicious actions. This may put the explorer in awkward or even dangerous situations. Rauwolf in 1542 when collecting plants on a hillside above Tripoli in Lebanon was suspected of taking note of the town's defences and was imprisoned. Linnaeus on his visit to Oeland in 1741 was likewise regarded as a spy. The Thomas brothers collecting for Haller in Switzerland were taken to be the scouts of sheep-stealers ! Fortunately medicine has provided many a botanist with a plausible alibi. In this connection it is entertaining to recall that when Sir Joseph Hooker visited the Atlas Mountains in 1871 with John Ball and George Maw he did so in the capacity of Hakim and Gardener to Queen Victoria, the Sultana of England, who, it was rumoured among the Moors, had heard that there was somewhere in Morocco a plant that would make her live for ever, and that she had sent her own doctor (hakim) to find it for her. ' When in the course of our journey it was seen that our botanical pursuits entailed rather severe labour, the commentary was : The Sultana of England is a severe woman and she has threatened to give them stick (the bastinado) if they do not find the herb she wants ! '

Botanical exploration calls for more than botanical knowledge. It calls for curiosity, zest, mental tenacity and a capacity to endure drudgery, hard work, discomfort and privation. It has to be encouraged intellectually, if not backed financially as well, by appreciative recipients of its hard-won material. Hence it may be said to reflect the mental climate of the time and the mental micro-climate of the individual. Moreover the means of travel to and into a given region necessarily regulate the work that can be done there. If, then, the amount of botanical exploration to the time of Linnaeus seems comparatively meagre, it should be balanced against the difficulties of travelling and the rarity of finding an eager, informed, tough individual with the desire and means to travel and the good fortune to return safely with his material, without being imprisoned, robbed, murdered, eaten or drowned, or enfeebled or slain by disease.

Greek Botanical Exploration

Botany as a science was fashioned out of herb-lore at Athens when Theophrastus (370–285 B.C.) applied to the vegetable kingdom the principles of classification based on logic associated with his teachers Aristotle and Plato. Embedded in Theophrastus's work, *The Enquiry into Plants*, are the results of the first recorded botanical exploration, the observations made on Alexander the Great's military expedition into Asia (Fig. 2) in the years 331 B.C.–323 B.C. In 331 B.C., after campaigning in Asia Minor and the Near East, Alexander marched eastward and defeated Darius south of Nineveh ; in 329 he turned northward into Turkistan ; in 327 he invaded India by the Khyber Pass and Chitral, went eastward to the River Beas, then turned to the south-west and reached the Indian Ocean near Karachi. From here some troops were sent homeward by sea under Nearchus. Alexander died in 323 B.C., but Greek interest in the East persisted ; in 290 B.C. a Greek embassy under Megasthenes visited the Indo-Gangetic Plain. The curiosity of the Greeks and their system of recording knowledge made Alexander's campaigning more than a military venture ; it became a scientific one, as did the expedition of the French army to Egypt in 1798 to 1801. The full reports transmitted to Athens have long been lost ; nevertheless out of the remnants preserved in Theophrastus's writings, Bretzl (1903) constructed a work of some 400 pages on the botanical results of Alexander's expedition. They illustrate a matter which deserves more attention, the stimulating and fertilizing impact of tropical Nature upon the keen and receptive analytic Western mind. It is an historical fact that science originated outside the tropics and a reasonable supposition that it could not have originated in them. Apart from tropical climatic conditions not being conducive to interlocked speculation and experiment and the evolution (as distinct from the transplanting) of social systems able to turn them to practical use, the diversity and complexity of Nature in the tropics forbid the construction of simple systems that must

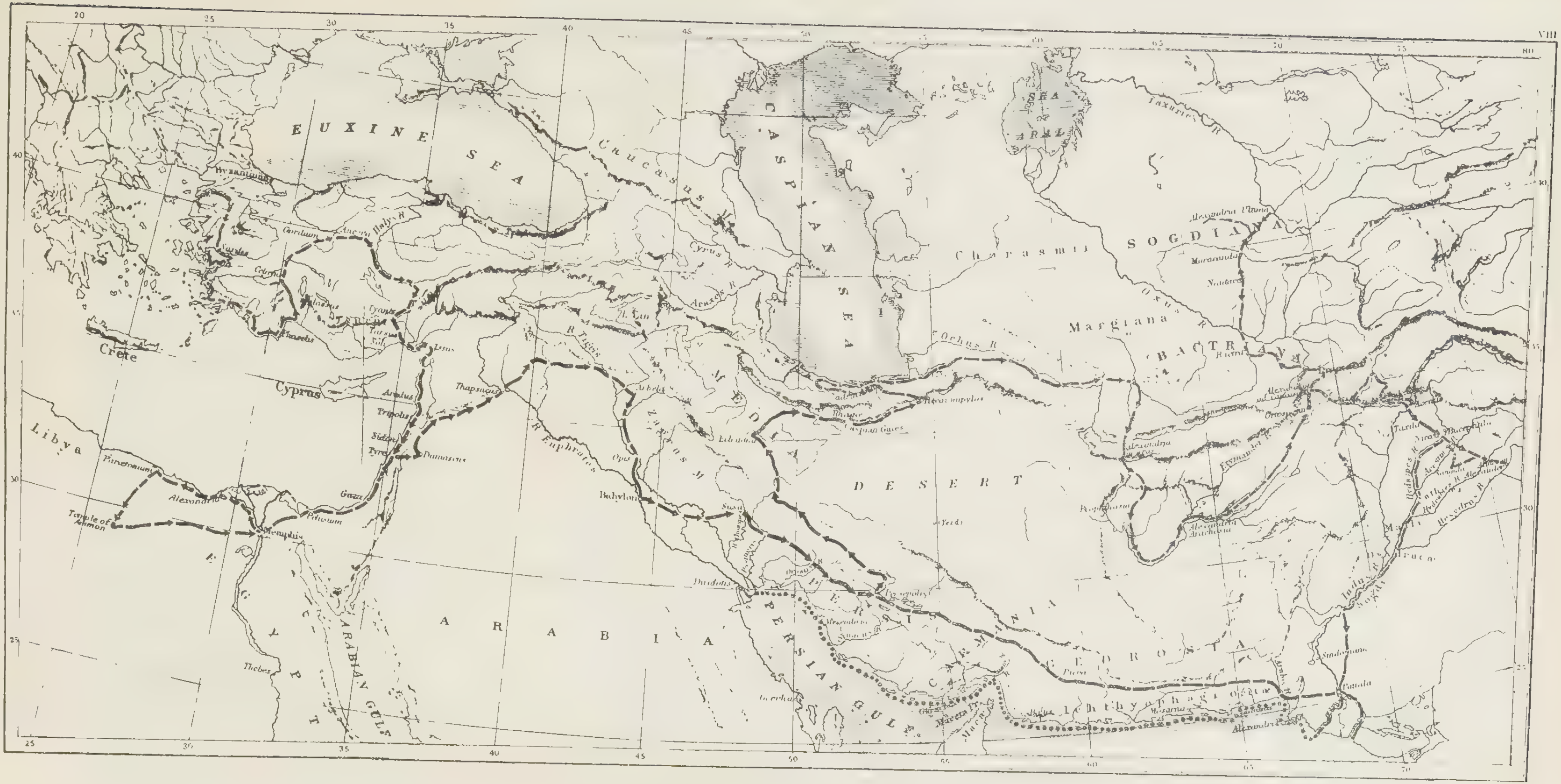

FIG. 2.—Alexander's campaigns in Asia (after Bunbury, 1879)

——→ route of Alexander . . . . voyage of Nearchus.

be basic to the development of complex ones. It was to Linnaeus's advantage that his botanical studies began with the plants of a few Swedish parishes and the then poorly stocked Uppsala botanic garden.

Greek penetration into India provided the raw material for plant geography. Crossing the Himalaya Alexander's men found high in the mountains an ivy (*Hedera nepalensis*) growing wild just as ivy grew wild in their native Hellas, but efforts to cultivate ivy in Babylon failed : ' the country does not admit the plant on account of the climate,' shrewdly observed Theophrastus. In North India itself they came across plants so astonishing that it required much more perspicacity to see them as counterparts of Greek plants. Thus bamboos (καλαμος ὁ ἰνδος) were regarded as giant reeds, the solid kind (*Dendrocalamus strictus*) being described as ' male ', the hollow kind (*Bambusa arundinacea*) as ' female '. Recognition of the banyan (*Ficus benghalensis* ; συκη ἡ ἰνδικη) as a kind of fig, despite its dissimilarity in habit, leaf and size of fruit to the cultivated fig (*Ficus carica* ; συκη), indicates real taxonomic insight. The description sent to Athens and preserved by Theophrastus is accurate and vivid :—' The Indian land has its fig-tree which drops its roots from its branches every year . . . from those of last year or even from older ones ; these take hold of the earth and make, as it were, a fence about the tree, . . . The roots as they grow are easily distinguished from the branches, being whiter, hairy, crooked and leafless. The foliage above is also abundant, and the whole tree is round and exceedingly large . . . the fruit is very small, only as large as a chick-pea, and it resembles a fig. And that is why the Greeks named this tree a " fig-tree " ' (Theophr., *Enquiry* IV, iv, 4 ; transl. Hort. **1** : 313). In the same reports occur the first references to the jack-fruit, banana and mango, as well as to many other plants different from those of Greece. They also include the first account of the mangrove vegetation of the Indian Ocean. ' On islands which get covered by the tide ', reported Alexander's men returning from India by sea, ' great trees grow, as big as planes or the tallest poplars, and it came to pass that when the tide came up . . . the branches of the biggest trees projected and they fastened the stern cables to them.' One of these maritime trees was described as having ' a leaf like that of the bay, and a flower like gilliflowers in colour and smell, and a fruit the size of that of the olive . . . and it does not shed its leaves.' This description clearly points to a species of *Avicennia*, probably that named *Sceura marina* by Linnaeus's Danish student, Pehr Forsskål, and now called *Avicennia marina*.

The Renaissance of Botany

Thus the Ancient Greeks made a promising start in botanical exploration and recording two to three hundred years B.C., but Greek science died in Europe and botany was not re-born there until the 16th century A.D. Its renaissance took place outside the Greek area. As stated by Burkill (1953), ' a system emerged out of the technology of healing in a particular part of Europe, was accepted and clad there with a vocabulary of precision, as sciences must be . . . this system has been spread over the world, India included, without meeting a rival. Its origin was, as it were, a sublimation in which " Man " was displaced from the focus of thought that the " plant " might be placed there.' To chart the area in which modern botany originated, Burkill marked on a map of Europe all the places known to him at which botanical books were printed from about 1500, the beginning, to 1623, the year of Caspar Bauhin's *Pinax*, since at this period ' the printing of a book is reasonable evidence of writing such in the neighbourhood ; the map, as it is based on all the botanical books printed to

Bauhin's time, represents the whole area of producing botanical work to 1623.' The delimited area (Fig. 3) extends northward, over Italy, from Naples and Salerno, to Montpellier, Lyons, Paris and London in the west, to Venice, Leipzig, Bautzen and Görlitz in the east, with Leyden and Amsterdam on its northern boundary. Within it are Bologna, Pisa and Montpellier, where the

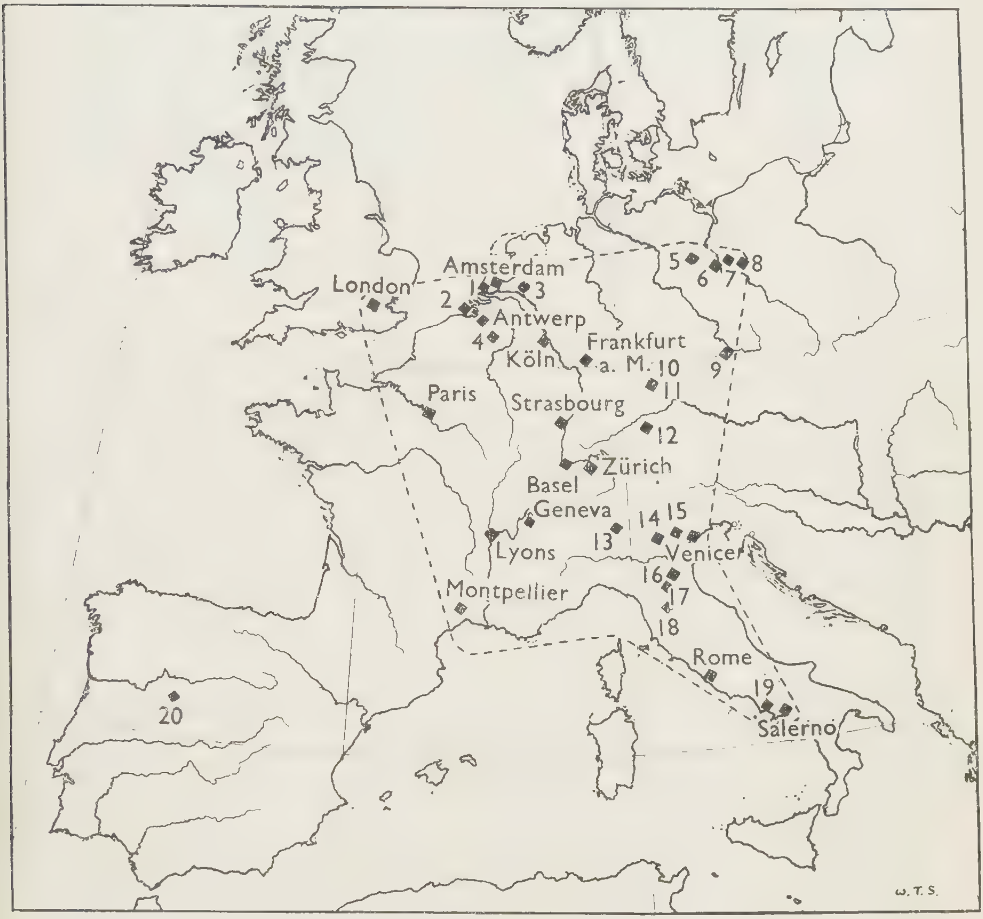

Fig. 3.—The area in which modern botany originated (based on Burkill, 1953). Places named are those where three or more botanical books were printed between 1500 and 1623. Numerals indicate places where one or two botanical books were printed :—1, Leyden ; 2, Middelburg ; 3, Arnhem ; 4, Louvain ; 5, Berlin ; 6, Leipzig ; 7, Bautzen ; 8, Gorlitz ; 9, Prague ; 10, 11, Nürnberg and nearby Altdorf ; 12, Augsburg ; 13, Bergamo ; 14, Mantua ; 15, Padua ; 16, Ferrara ; 17, Bologna ; 18, Florence ; 19, Naples ; 20, Salamanca. Bologna under Luca Ghini and Montpellier under Rondelet were important centres of botanical teaching.

two most influential botanical teachers of the period, Luca Ghini (1490–1556 : cf. Chiarugi, 1957) and Guillaume Rondelet (1507–66 ; cf. Planchon, 1866), lectured to students attracted from many countries. It expresses the too easily overlooked cultural unity of Europe that produced modern science. For a thinker and observer to be effective, i.e. to influence human thought and action directly, his work must come to the attention of an understanding appreciative public. The Renaissance, the Reformation, the Counter-reformation and the invention of printing had created in Europe by the early 16th century a small but international mutually stimulating and scientifically interested public of learned men. The growth of this intellectual community and the extension of its activities beyond Europe are the background to botanical exploration. By their correspondence and their publications, men like Ray, Petiver and Sloane in England gave purpose to the labours of collectors isolated like Kamel in the Philippines, Cuninghame in China, and Banister in Virginia. The spread of botany outside its area of origin, an area occupied by Italians, French, Swiss, Germans, Dutch, Flemings and English, owes something to Jewish activity. Thus one small book is credited to Salamanca in Spain, long a centre of Jewish learning, and another to Goa in India where in 1563 Garcia d'Orta (*c.* 1490–1568), himself a graduate of Salamanca, who as a Marrano (secret Jew) had settled in India away from the Inquisition, published his mainly pharmacological but partly botanical *Colloquios dos Simples e Drogas . . . da India* (cf. Seide, 1953 ; Friedenwald, 1944). Spring comes late, but with stimulating freshness, in the north ; Sweden, Linnaeus's country, lay outside the area of 16th century botanical work and publishing.

Botanical exploration began within this area by herbalists, searching their homelands for plants which they could identify with the medicinal herbs of the Ancients, notably those listed by the Greek herbalist Dioscorides (cf. Arber, 1938). They did not find the same plants, for Central Europe and Italy have floras distinct from those of the Eastern Mediterranean, but they often thought they had and thereby misapplied many classical names in a manner which Linnaeus perpetuated. With so much to learn at home they felt no great urge to go simpling abroad. There is thus a marked contrast between the amount of botanical exploration outside and inside Europe down to the time of Linnaeus, and at the present time the contrast, though now much less striking, still remains.

Early Botanical Travellers

It is instructive to mark on a world map those areas outside Europe where enough collecting or recording had been done by 1732 to provide specimens or published descriptions or illustrations of plants which Linnaeus could use, i.e. which gave him enough information for the plants concerned to be assigned a definite place within his system of classification. Such a map (Fig. 4), with the names of the travellers responsible added, shows that, although these areas were small and the men comparatively few, they brought within his ken a selection of plants from lands as remote as Japan, coastal China, the Philippines, Ceylon, Southern India, the Cape of Good Hope, Brazil, Chile, Peru, Jamaica, Virginia and eastern Canada. He thus had before him representatives of ten out of the 37 floristic regions into which a modern plant-geographer (Good, 1953 : 29–31, pl. 4) divides the globe. None of the men who visited them was a professional botanist, for botany had not yet grown to be an economically independent science. These early botanical travellers were mostly physicians and priests interested primarily in medicinal plants, i.e. those whose properties were already known to native peoples ; to find plants new to Europeans they had no need to penetrate virgin forest. Hence their collections come mostly from coastal regions, not from the deep interior. Seemingly indifferent to financial reward, they possessed in good measure that restless curiosity which, by leading to technological superiority, made possible European expansion overseas. As men they were as varied as human nature, learned like Kaempfer, gentle like Rumpf, quarrelsome like Samuel Browne, and so on, but they all had perseverance, enthusiasm and stamina. They needed all three.

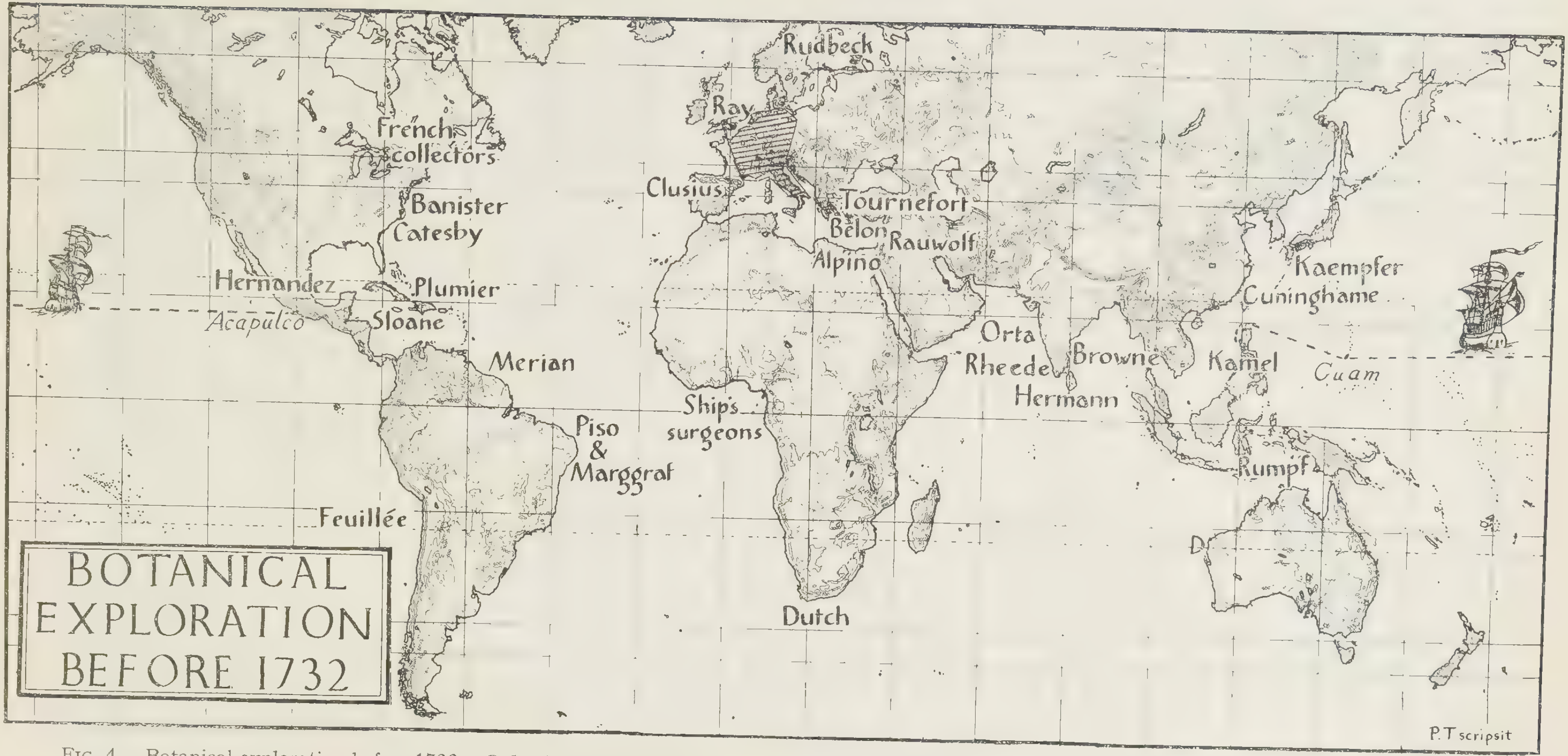

FIG. 4.—Botanical exploration before 1732. Only the more important collectors who supplied illustrations or specimens available to Linnaeus are named, and their areas of activity indicated. The two galleons indicate the eastward route of the Acapulco-Manila galleons, the letter 'D' the coast of Western Australia visited by Dampier in 1699. The hatched area of Europe is that wherein modern botany originated (cf. Fig. 3).

Misfortune attended many of the early botanical travellers as it did other travellers then. In his *Critica botanica*, no. 238 (1737), Linnaeus discussed generic names formed to preserve the memory of botanists who had deserved well of the science and he gave instances of men who had suffered hardship, risked their lives, spent laborious days and sleepless nights in pursuit of botanical knowledge. It is an interesting list. The first of the botanical heroes on Linnaeus's list is Linnaeus himself: ' in my youth I enter the deserts of Lapland . . . I live only on water and meat . . . I risk my life on Mount Skula, in Finmark, on icy moutains, or from shipwreck, or among the clouds ; travelling afoot I penetrate forests and alpine regions ; and all in order that I may gather the plants of the poverty-stricken Lapland Flora '. The others include the Scheuchzers, Tournefort, Charles de l'Escluse (Carolus Clusius), Cluyt (Clutius), Wieland (Guilandinus), Rumpf (Rumphius), Barrelier, Micheli, Hermann, Oldenland, Plumier, Marggraf (Marcgravius), Lippi and Banister, and some others such as Plukenet, ' who prefers plants to riches ' but can hardly be rated as a botanical explorer or martyr !

Botanical Travellers in Britain

The activities of these early botanical travellers touched all the continents, except Australia,[2] and it is convenient to deal with them briefly, continent by continent. In Europe by 1732 many regions had already been covered by local lists, admittedly not so detailed as later works but good enough to indicate the general nature of the flora. These pioneer works rested upon both long and hazardous journeys and short excursions made around centres of learning or commerce. In England, for example, early in the 17th century, it was not unusual for London doctors and apothecaries to make ' a public excursion and simpling-tour ', as mentioned by l'Obel. Of these the most entertaining seems to be one by Thomas Johnson (*c.* 1600–44) and nine other apothecaries, who set out at break of day from St. Paul's Cathedral on 13 July 1629 upon a journey into Kent. They embarked on the Thames in two boats for Gravesend, were nearly shipwrecked in a storm, but reached Chatham and crossed to Queenborough. This village had only one street but two inns and a mayor, who, by virtue of ancient privileges and responsibilities for public safety resting upon his office, demanded to know the purport of their visit. One of the party diplomatically explained that, independently of their herborizing, the pleasure of seeing so eminent a man as the Mayor of Queenborough, a man well known to be versed in nautical affairs, would have been a sufficient inducement for their coming, and the episode closed with all drinking healths in excellent ale. Having occasions such as this in mind a Cambridge botanical lecturer about 1950 stipulated that Clapham, Tutin and Warburg's then forthcoming *Flora of the British Isles* (Cambridge University Press, 1952) should be provided with a beer-proof binding ! The result of the apothecaries' trip was a list of Kent plants, described by Raven (1947 : 275) as ' an excellent beginning of a local flora ', as well as a racy account of field-botany, Thomas Johnson's *Iter Plantarum Investigationis . . . in Agrum Cantianum* (1629). Johnson's determination ' to travel over the most parts of this Kingdome in search of plants' took him through some 33 botanical vice-counties (cf. Kew & Powell, 1932 : 137) before a musket shot at the siege of Basing House in 1644 ended the career of this gallant Royalist and pioneer of British field-botany.

The work of Johnson in exploring Britain botanically was carried on by John Ray (1627–1705 ; cf. Raven, 1942) who wrote in February 1659 ' to friends and acquaintances who are skilful in Herbary to request them this next summer to search diligently his country for plants' and himself made a succession of botanical journeys. These took him to Derbyshire and North Wales in 1658, to northern England and the Isle of Man in 1660, to northern England and southern Scotland in 1661, to Wales and Cornwall in 1662, to the continent of Europe in 1663 to 1666. On this grand tour he visited the Low Countries, Germany, Austria, Italy, Sicily, Malta, Switzerland and France. Such journeys provided Ray with a detailed first-hand knowledge against which he could check and assess the records of others. Thus they are basic to the works on which Linnaeus relied for much of his information about the distribution of European plants, Ray's *Historia Plantarum* (1686–1704) and Ray's *Synopsis methodica Stirpium Britannicarum* (1690 ; 3rd ed., 1724).

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[2] See Footnote 1, p. 174.

BOTANICAL TRAVELLERS ON THE CONTINENT OF EUROPE

Of earlier travellers in Europe for botanical purposes, first place goes to Conrad Gesner (1516-65) of Zürich, not only for his own travels and his encyclopaedic learning but also for his help and encouragement to others, notably William Turner, Thomas Penny, who collected in the Balearic Islands and gave Clusius information, and J. Bauhin. In 1555 Gesner made a notable exploration of the Pilatus Berg, near Lucerne, the ascent of which was then rigidly controlled by the Burgomaster of Lucerne lest objects thrown into the Pilatus See should arouse the thunderous wrath of Pontius Pilate ! His publication, *Descriptio Montis Fracti sive Pilati* (1555), not only contains the first list of alpine plants but distinguishes zones of vegetation (cf. Mägdefrau, 1938). Here is the source of Linnaeus's generic name *Trollius*, derived from Gesner's latinization as ' Trollius flos ' of the local name ' Trollblume ' (cf. Stearn, 1941). In 1561 he made a journey with young Johann (Jean) Bauhin (1541–1613) through the Rhaetian Alps and the Val Tellina, the key route between Austria and Italy. They found many species later described by J. Bauhin and his brother Caspar, among them a little plant named *Campanula serpyllifolia* by C. Bauhin in 1596 and *Linnaea borealis* by Linnaeus in 1753. Gesner was in many ways a pioneer : ' I have determined, as long as God gives me life, to ascend one or more mountains every year ', he wrote in 1541, ' when the plants are at their best—partly to study them, partly for exercise of body and joy of mind ' (cf. Raven, 1953 : 88).

Unfortunately, owing to Gesner's death from bubonic plague in December 1565, little of his botanical work was ever published, although to illustrate it he had brought together some 1500 drawings. J. Bauhin likewise never lived to see the publication of his own vast work, the *Historia Plantarum universalis* (1650–51). As an achievement of the period this is only to be compared with the *Pinax* (1623) by his brother Caspar (Gaspard) Bauhin (1560-1624). The genus *Bauhinia*, ' with two-lobed leaves, or two as it were growing from the same base, being called after the noble pair of brothers Bauhin' (Linnaeus, *Crit. bot.*, no. 238), was thus aptly named by Plumier. Caspar travelled widely in Europe and amassed an important herbarium, now at Basel, which contains material from the correspondents and friends listed at the beginning of his *Prodomus* and *Pinax*.

Among these is ' Joachimus Burserus, medicus Annaebergensis ', a German doctor Joachim Burscher (1583 1639), better known as Burser, of whom Legré (1904 : 71) has remarked ' on trouve peu de botanistes qui aient herborisé avec une telle activité '. He too formed a big herbarium, now at Uppsala (cf. Stearn, 1957 : 116–118 ; Juel, 1936). His travels in the Austrian and Swiss Alps as well as in Provence, Languedoc and the Pyrenees resulted in the discovery of new species and he communicated his material to Bauhin. Thus, as Spencer Savage (1937) has emphasized, there came to be so close a correspondence between their herbaria that Burser's can be used to interpret Bauhin's *Pinax* in accordance with which it is arranged. Burser settled in Denmark in 1625.

His herbarium, which included a few Canadian specimens (cf. Juel, 1931) was taken by the Swedes as war-booty in 1657 58 and ultimately reached Uppsala where first the two Rudbecks and then Linnaeus made much use of it (cf. Stearn, 1957 : 116–118, 127–128).

The investigation of the natural history of the Alps begun by Gesner and carried on by Penny, the Bauhins and Burser was energetically renewed at the end of the 17th century by the brothers Johann Jacob Scheuchzer (1672–1733) and Johann Scheuchzer (1684–1738). The contemporary attitude towards mountains, grim forbidding barren places, finds expression in the plates of J. J. Scheuchzer's book. Travelling through the Alps possessed for J. J. Scheuchzer an excitement that no modern traveller can share with him ; the likelihood of being confronted suddenly by a dragon leaping down from the rocks was always in his mind ! His *Ouresiphoites Helveticus* (Iter alpinum quintum ; 1723) gives in all seriousness no less than 11 pictures of these monsters based on seemingly accurate reports and the bones of extinct animals found in Switzerland, so that they are, in a sense, far-fetched palaeontological reconstructions! The works of his brother are mainly concerned with Gramineae and Cyperaceae. Hence, to quote Linnaeus, *Critica bot.*, no. 238 (1737), ' *Scheuchzeria* is grassy and alpine, being called after the famous pair of brothers Scheuchzer, of whom the one was eminent for his knowledge of grasses, the other for his knowledge of alpine plants '.

The most important contributions of the period to the botany of the Iberian Peninsula and of Hungary were both made by Clusius (Charles de l'Escluse, 1526–1609), a Fleming, in many ways the most remarkable botanist of his time. As Arber (1938 : 85) has truly said, ' the misfortunes which Charles de l'Ecluse suffered, would have crushed most men, but he rose above them, finding his happiness in his inexhaustible capacity for work, and in his power of forming friendships, wherever he went, with men of learning '. In 1564, while tutor to two boys, Johann and Markus, of the rich Fugger family, he made a journey through Spain and Portugal, discovering some 200 new species of plants. They were not acquired without risk and pain. He fell with his horse down a precipice, breaking his right arm ; on another occasion he damaged a leg. Clusius published the botanical results of this journey in his *Rariorum aliquot Stirpium per Hispanias observatarum Historia* (1576 ; cf. Christ, 1912). In 1573 Clusius was invited to Vienna to take charge of a garden for the Emperor Maximilian II who died in 1576. The next Emperor, Rudolf II, had no love for Protestants ; so Clusius lost his position at the Court and had to leave Vienna almost destitute but received protection from an Hungarian baron, Balthasar de Batthyány. His travels in Austria and that part of Hungary not under Turkish rule resulted in his *Rariorum aliquot Stirpium per Pannoniam, Austriam et vicinas quasdam Provincias observatarum Historia* (1583 ; cf. Christ, 1912–13), the first flora of the region. In 1581 he visited London and came to know Sir Francis Drake. In 1593 the Dutch invited him, though now an infirm old man, to their newly instituted University of Leyden ; from here in 1601 he published his *Rariorum Plantarum Historia*, bringing together in one profusely illustrated folio volume the results of his travels.

The far north of Europe received little botanical attention until nearly a century later, when King Charles XI of Sweden put in hand the investigation of Lapland. At his command Olaus Olai Rudbeck (1660–1740), son of O. J. Rudbeck, journeyed in 1695 to Lule Lapland (cf. Fries, 1898). The scientific results of his travels would have been important had they been immediately published. Unfortunately the disastrous Uppsala fire of 1702 destroyed almost all the material that Rudbeck and his father had so laboriously assembled. It took the heart out of Rudbeck for such work. Years later he found an eager listener to his Lapland reminiscences in a student acting as tutor to some of his 24 children. That student was Linnaeus. As they sat by the fire, the old man's romantic description of the unexplored Lapland wilderness, the wealth of flowers, the ways of the Lapps, must have aroused in the young one a burning desire to go to Lapland and be its chronicler. In May 1732 he blithely set off on his Lapland journey. In 1737 he published his *Flora Lapponica*. The tree that King Charles XI had planted in 1695 had taken a long time to come into bearing but its yield thereafter was bountiful.

Botanical Exploration in the Americas

Although fruitful botanical exploration outside Europe before 1732 is mostly a by-product of the overseas commercial and imperial expansion of the Dutch and English peoples backed and stimulated by influential scientifically minded persons in Holland and England, the Spanish and Portuguese were first in the field (cf. Howe, 1946 ; Penrose, 1952). Considerations of security, the fear of revealing to heretical and jealous other European powers the sources of their wealth, restricted their contributions to the world pool of knowledge. They acquired their far-flung empires and were ruined by them, Spain by too much American gold and silver too easily obtained and too easily dissipated, Portugal by the scattering and loss of her manpower, before the marked development of the natural sciences in northern Europe during the second half of the 17th century provided a spur other than economic gain for the investigation of their territory. Moreover the strong individuality of the Spaniards, leading so often to strife among themselves, made sustained co-operative effort difficult. Great plans and the devotion to duty of idealistic hard-working individuals in Spanish domains came to naught through jealousy and apathy ; there existed in Spain no enlightened effective public opinion to support them. The history of Francisco Hernandez (d. 1558), personal physician to King Philip II of Spain, provides an example. Linnaeus, when indicating links by which to connect generic names with the plants concerned (cf. *Critica bot.*, no. 286) and thereby more easily to memorize the association, stated that ' *Hernandia* is an American tree, with the handsomest leaves of any, and less conspicuous flowers—from a botanist who had supreme good fortune and was highly paid to investigate the natural history of America : would that the fruits of his labours had corresponded to the expenditure !' This remark does less than justice to Hernandez, who received in truth a raw deal. In 1570 he went out to New Spain (Mexico) ; by 1575 he had with astonishing industry compiled 16 folio volumes on its plants and their medicinal properties ; he returned to Spain in 1577 and died the year after. A Latin manuscript left behind in Mexico was published there (in a Spanish translation) but not until 1651 was his *Rerum medicarum Novae Hispaniae Thesaurus* given to the world ; in 1671 a fire in the Escorial destroyed his manuscripts and drawings.

South American botany was known to Linnaeus chiefly from three works. The *Metamorphosis Insectorum Surinamensium* (1705) by Maria Sibylla Merian (1647–1717) is primarily an entomological book but Merian portrayed her butterflies, moths and caterpillars as feasting or resting upon a variety of tropical plants growing in Dutch Guiana. This couragous and enterprising artist and her daughter made the long tedious voyage to Paramaribo simply to collect and paint tropical insects and plants, which for the period was an astonishing act.[3] Two years later they had to return to the Netherlands on account of her health, but Johanna, the daughter, went back later to Surinam and sent home further drawings and specimens. There is nothing characteristic of the wild flora of

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[3] For some notes on the high death-rate aboard Dutch ships, see T. J. Arne, ' Svenska läkare och fältskärer i holländska Ostindiska Kompaniets just ', *Lychnos*, **1956** ; 132–146 (1957).

Surinam in Merian's splendid plates; they furnished European botanists, however, with a series of coloured pictures of such economic plants as the pineapple, cassava, pomegranate, cotton, guava, cashew, lime, shaddock, pawpaw, banana, passion fruits, soursop and castor-oil plant, even though, particularly when considered from the entomological standpoint, the book, to quote Guilding (1834), 'abounds in errors against which the naturalist in Europe should be always upon his guard'. Much earlier than this, when the Dutch and Portuguese were struggling for Brazil, Willem Piso (fl. 1635–58) and Georg Marggraf (1610–44) assembled many notes on medicinal plants in north-east Brazil (between 5° and 11° S.) which formed the basis of their *Historia naturalis Brasiliae* (1648). They arrived in Recife (then Moritzstadt) in 1637, made many journeys and exploration into the interior (Ceara, Rio Grande do Norte, Paraiba, Pernambuco, Alagoas, Sergipe, Bahia) and returned to Holland in 1644. In 1858 Martius published a commentary on their cryptogams.

Between 1707 and 1712 a French monk, Louis Feuilleé (1660–1732), like Plumier a Minime brother, surveyed the western coast of South America by making many 'Observations physiques, mathematiques et botaniques', which are illustrated in his published *Journal* (1714–25) with many excellent engravings; this contains his *Histoire des Plantes médicinales de Pérou et Chile*, upon the illustrations and descriptions of which Linnaeus, Jacquin and Savigny later based specific names.

For the West Indies the most important pre-Linnaean works are those of Charles Plumier (1646–1704), a French monk, and Sir Hans Sloane (1660–1753), a successful Irish physician of Scottish descent whose collections form the basis of the British Museum. Sloane went out to Jamaica in 1687, reaching the island in December 1687, and left it reluctantly in March 1689. His work as a physician naturally limited his opportunities for botanizing but he used them with much zeal and published the results in two thick volumes so full of first-hand information and so profusely and accurately illustrated that even to-day the critical student of West Indian plants must refer to his plates and descriptions and the material in the British Museum (Natural History) on which they were based (cf. Dandy, 1958). The first volume of his *Voyage to the Islands Madera, Barbados . . . and Jamaica* appeared in 1707, the second in 1725. Clifford obtained the services of Linnaeus from Burman, whom Linnaeus had undertaken to help, by giving Burman a copy of the second volume of Sloane's *Voyage* in exchange!

Charles Plumier reached the West Indies later than Sloane but stayed there longer and well deserves the first place among the fathers of Antillean botany accorded him by Urban (1920), not only for the large number of new genera and new species discovered by him but for the excellence of his descriptions and drawings. He went out to the French islands in 1689 accompanied by Joseph Donat Surian (d. 1691). The latter collected specimens, which are now in Paris; few of Plumier's have survived (cf. Dandy, 1958 : 188)—probably most were lost in a shipwreck—but he certainly drew them with skill. Plumier's first journey was in 1689–90, his second in 1693, his third and last in 1696–97. He spent most of his time in Haiti, the eastern and French part of Hispaniola, floristically an exceedingly rich island. His drawings in Paris are said to number nearly 6000, some being coloured. Copies made by Aubriet for Boerhaave came after the latter's death into the hands of Burman—they are now at Groningen—and from these Burman had rather crude engravings made for publication. On them Linnaeus based accounts of many West Indian species otherwise unknown to him . A few are still known only from Plumier's drawings; in 1920 about 50 of Plumier's flowering plants and 30 of his ferns had yet to be matched with modern specimens. This is because the flora of Hispaniola, like that of Cuba and of Jamaica, is rich in species of limited distribution, and collecting there has been far from adequate despite the remarkable work of Erik Leonard Ekman

(1883–1931). Thus *Ipomoea digitata*, named by Linneaus in 1759 (*Systema Naturae*, Ed. 10, **2** : 924) from Burman's 1756 reproduction (*Plant. Amer.*, **4** : 81, t. 92 f. I, as *Ipomoea foliis pedatis*) of a drawing made by Plumier between 1689 and 1697, remained otherwise unknown[4] until Ekman came across it in Haiti in 1924 (cf. Urban in *Archiv f. Bot.* **20** A, no. 5, 42 ; 1926). Plumier revived the Greek custom of naming genera after persons, which Linnaeus enthusiastically adopted, although credit for this should perhaps go also to Rabelais with his herb Pantagruelion !

As a consequence of the French settlement in Canada, following the voyage of Jacques Cartier (cf. Rousseau, 1937) and the English settlement in New England and Virginia, a number of Eastern Northern American plants found their way to the gardens of the settlers' homelands of France and England. Many were sent or brought back by persons now unknown. The period from about 1600 to 1680 is indeed termed ' der Zeit der canadisch-virginischen Stauden ' by Gregor Kraus (1894) in his history of the introduction of plants into European gardens. A few herbarium specimens, apparently sent at the same time from New France, were acquired from an apothecary in Paris by Burser (cf. Juel, 1930) and communicated by him to Caspar Bauhin, who enumerated them in his *Prodromus* (1620). Burser and Bauhin supposed them to have come from Brazil. Despite the imperfect phytogeographical knowledge of the time Linnaeus recognized them as Canadian ; with like astuteness he separated the Ceylon from the Cape specimens in Hermann's collection. In 1635 J. Cornut published an account of about 40 species from Canada cultivated in Paris, *Canadensium Plantarum aliarumque nondum editarum Historia*. Other plants of North American origin were figured by Plukenet, Morison and Hermann and in this way made known to Linnaeus. Of pre-Linnaean collectors in Virginia the most energetic was John Banister, a missionary who met his death in a climbing accident about 1692. He sent descriptions and drawings, specimens and seeds to his friends in England ; unfortunately Plukenet was only able to publish a few engravings made from Banister's beautiful drawings, which are now in the British Museum at Bloomsbury, and Banister's contribution to a knowledge of the North American flora, which could have been extensive, was thus ineffectual. More important because published with illustrations and used by Linnaeus, is the work of Mark Catesby (1682–1748 ; cf. Allen, 1937), described by a contemporary as ' a gentleman of small fortune . . . pretty well skilled in Natural History ', who went out to Carolina in 1722. After three years there and in Georgia and Florida collecting and drawing, Catesby visited the Bahamas. Between 1731 and 1747 he published his *Natural History of Carolina, Florida and the Bahamas Islands* (cf. Stearn, 1958) illustrated rather quaintly and crudely by himself. Linnaeus unfortunately overlooked Catesby's visit to the Bahamas and attributed a number of Bahama species to Carolina, even naming one of them *Ipomoea carolina* ! During Linnaeus's lifetime knowledge of the eastern North American flora grew rapidly. According to Juel (1920), Linnaeus came to know about 780 species of plants characteristic of North America, of which about 100 were unknown to earlier authors.

Botanical Exploration in Africa

Africa was long regarded by European nations as primarily an unfortunate obstacle in the way of ships trading with the East Indies. ' Could Africa cease to exist ', wrote Hugh Murray in 1844, ' great facilities would be afforded to communications between the other continents, and many new channels of commerce be opened up '. Tropical Africa produced no spices except pepper; it was hot and unhealthy, disease-ridden and inhabited by strange beasts, hostile slave-raiding Mohammedans and pagan savages; indigenous African cultures and kingdoms were to be despised as forms of barbarism; the coasts offered few good harbours; apart from some gold and ivory, Africa's chief wealth seemed to lie in the slaves, mostly prisoners of war, which African chieftains were only too willing to bring to the coast and sell. Scientifically minded Europeans of the pre-Linnaean period thus had little incentive to penetrate the dangerous interior. Consequently geographers on their ' Afric-maps ' could do little but

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[4] The correct name for the species commonly known as *I. digitata* seems to be *I. mauritiana* Jacq.

' o'er unhabitable Downs
Place Elephants for want of Towns,'

as Swift wrote, and the flora of tropical Africa remained unknown, apart from a few scraps of specimens given to Petiver by surgeons at the slaving stations of the West Coast, until the latter part of the 18th century when, under the inspiration of Linnaeus, his students Berlin and Afzelius made the first important collections there. In London as early as 1719 a group of persons interested in natural history planned to send a naturalist to tropical Africa but apparently no-one then had any great desire to go to that ' sickly place '.

The first settlements at the Cape of Good Hope were established to provide a port of call where ships could revictual on their way between Holland and the spice islands of the East Indies. By chance, however, they were made within a region with so rich and distinct a flora that it is recognized by plant-geographers as a floristic kingdom. The beautiful and strange plants of the Cape invited introduction at once into European gardens. The first to arrive seems to have be *Stapelia variegata*, sent to Holland by Justus Heurnius, a clergyman travelling to the Dutch East Indies, and illustrated in 1644 by J. Bodaeus à Stapel in a commentary on Theophrastus! In 1652 Jan Anthonisz van Riebeeck founded the colony that became Cape Town and the making of a garden was among his first tasks. From here, particularly during the governorship of Simon van der Stel and his son, Wilhem Adriaan van der Stel, and the superintendence of the Dutch East India Company's garden (cf. Karsten, 1951) by Heinrich Bernhard Oldenland (d. before 1699) and Jan Hartog, many new plants soon found their way to Holland. There, in a living state and through illustrations in the works of the Commelins and Hermann, these plants came to the attention of Linnaeus.

BOTANICAL EXPLORATION IN ASIA

Economically far more important to spice-wanting Europeans than South Africa were Ceylon, India, Java and other Indonesian islands. Here the Dutch followed the Portuguese. In 1669 Hendrik Adriaan van Rheede tot Draakenstein (1637–92) became Governor of the Dutch possessions along the Malabar coast of Southern India and set in hand their botanical investigation. He seems to have been the first to record the extraordinary diversity of trees in tropical woodland and the wealth of epiphytes: ' it would be difficult to obtain two trees of the same kind in one forest . . . on one tree ten or twelve different sorts of leaves, flowers and fruits might be met with ' (cf. Witt, 1949: lxxxiii). He was the first to realize the need for team work in the preparation of a tropical flora. He collected himself, in association with an Italian missionary Mattheus, but ultimately employed a staff of about 16 learned Brahmins and four artists. who described and drew the living plants brought from parts of Cochin by native collectors. From the Malabar vernacular the descriptions were translated into Portuguese and from that into Latin, then sent along with the drawings to Holland, where they were edited and published by A. Syen and Jan Commelin as the *Hortus Indicus Malabaricus* (12 vols., 1678–1703). They provided Linnaeus with most of his information about the flora of India.

They also provided the Linnean Society with material for its meetings during the dullest period of its existence. As stated by Gage (1938 : 114), Francis Buchanan, afterward Hamilton, ' wrote an erudite and prodigious " Commentary on the Hortus Malabaricus " which he presented to the Society . . . Very occasionally the reading of a paper occupied the whole or part of the hour at more than one meeting, but Hamilton's Commentary stands by itself, for the Society was doped with it at 31 meetings, the first dose being given in May 1821 and the last in April 1852 ! '

The Dutch at the time of Rheede's activity also held coastal Ceylon. In their employ Paul Hermann (1646–95), a German doctor from Saxony, reached Ceylon in 1670 ; he made a herbarium, as well as a collection of drawings, of plants occurring near Colombo, and these he took to Holland, when in 1680 he became a professor at Leyden. Later his specimens and drawings were lent to Linnaeus, who based his *Flora Zeylanica* upon them. The flora of that part of Southern India under British control, the Madras coast, received about this time some attention from surgeons of the Hon. East India Company, Richard Sambach (fl. 1698–1727), Samuel Browne (d. before 1703) and Edward Bulkley (*c.* 1651–1714), who collected specimens for the London apothecary James Petiver and, he figuring some of them, they became known to Linnaeus. These collectors did not give their finds much study. As Burkill (1953 : 851) has said, ' Samuel Browne was indeed no student, and was a source of trouble to Authority from being quarrelsome, arbitrary and a dueller. Once he found himself in jail from which he got early release because he was needed to look after his patients. Once he had the misfortune to poison a patient with arsenic because his apparatus for preparing his medicines was not kept as it should have been '.

Trading visits to the coast of China enabled a surgeon in the East India Company's employ to send material from there to Petiver. Large collections were thus made between 1698 and 1707 at Chusan, Amoy (Emuy) and the Dog Islands (Linnaeus's Insula Crocodilorum) near Fuchow by James Cuninghame (d. *c.* 1709), who also visited Cochin-China. According to Bretschneider, about 600 Chinese species of his gathering are described by Petiver and Plukenet, some 300 being figured. Thus these plants came under the eye of Linnaeus. He referred a number to species he already knew from other material but three Linnaean species, i.e. *Acrostichum dichotomum*, *Menispermum orbiculatum* and *Sagittaria trifolia*, are entirely based on illustrations of Cuninghame's plants. The interior of China did not become known botanically until the second half of the 19th century.

Petiver's acquisitive enthusiasm (cf. Stearns, 1952 ; Dandy, 1958) links Browne with a Moravian German apothecary in the service of the Society of Jesus, Georg Joseph Kamel (1661–1706), resident at Manila in the Philippines from 1688 until his death.

All three were in correspondence. As is evident from the biography of Kamel by J. & R. Gicklhorn (1954), he must have received a thorough training in pharmacy and hence in the botany of the time before going to the Philippines. He was the first to give the natural history of these islands scientific attention. He sent numerous specimens, drawings and descriptions to his English correspondents, notably Petiver, Ray and Samuel Browne. Chinese pirates infested East Indian waters and he lost the results of ten years' labour in one day when a ship carrying his herbarium fell into their hands. Like his contemporaries Kaempfer, Plumier and Banister he was a fine draughtsman ; it is regrettable that so few of their drawings were published. Unfortunately Linnaeus, having no access to Kamel's original drawings or specimens, could cite only such of his plants as were figured by Petiver. The descriptions given in Kamel's ' Historia

Stirpium Ins. Luzonis et reliquarum Philippinarum ', printed in the Appendix to volume 3 (1704) of Ray's *Historia Stirpium*, were useless from Linnaeus's standpoint since they did not give the floral details basic to the Linnaean sexual system of classification and hence the plants concerned could not be satisfactorily allocated to Linnaean genera. Nevertheless Linnaeus's dedication to him of the genus *Camellia* has brought him an unexpected though far from unmerited fame.

Camellia itself was unknown to Kamel. Linnaeus based his account not on information published by Kamel but by Engelbert Kaempfer (1651–1716), a learned Westphalian German doctor from 1688 to 1693 in the employ of the Dutch East India Company. Kaempfer was born in the little north German town of Lemgo ; it suffered during his youth from a reign of terror and witch-mania, which is graphically described in Karl Meier-Lemgo's novel *Der Hexenbürgomeister von Lemgo* (1951), and probably for this reason he received his schooling elsewhere, in Lüneberg, Hamburg and Lübeck. In 1680 he went to Sweden. Between then and his return to Germany in 1694 he travelled across Russia to Persia, then joined the Dutch East India Company's fleet as a surgeon, visited Ceylon, Bengal and Java and in September 1690 reached Nagasaki, southern Japan. Here the Dutch were confined to a little artificial island, Deshima, in Nagasaki harbour. Once a year the Dutch ambassador and his retinue travelled to Yedo, now Tokyo, to pay homage to the Shogun. The journey (Fig. 5) took about two months and Kaempfer made it twice, in February to May 1691 and March to May 1692. He left Japan in October 1692 and returned to Europe, spending the rest of his life at Lieme near Lemgo as a country doctor. The close restrictions upon foreigners in Japan made it impossible for Kaempfer to botanize in Japan as he had done during his three years in Persia. By supplying his Japanese interpreters with instruction ' in astronomy and mathematicks, and with a cordial and plentiful supply of European liquors ', he overcame their reluctance to reveal information about Japan and they brought him numerous specimens of plants cultivated or growing wild around Nagasaki (cf. Stearn, 1948). These he drew with skill. The frustrations of his home-life at Lieme (cf. Meier-Lemgo, 1937) deprived the world during his life-time of much of the results of all this travel, observation, note-taking and drawing. Not until four years before his death did he succeed in publishing his remarkable *Amoenitatum exoticarum politico-physico-medicarum Fasciculi* (1712). The engravings in this book represent the species which Linnaeus later named *Morus papyrifera* (p. 473), *Uvaria japonica* (p. 447), *Thea sinensis* (p. 606), *Ficus pumila* (p. 805), *Ginkgo biloba* (p. 811), *Taxus nucifera* (p. 814), *Bignonia Catalpa* (p. 842), *Azalea indica* (p. 847), *Camellia japonica* (p. 851), *Epidendrum moniliforme* (p. 865) and *Kaempferia Galanga* (p. 902), as well as other species named by Linnaeus's student Thunberg. The strange name *Ginkgo* originated apparently as a printer's misrendering of Kaempfer's ' gin kjo ' (i.e. *gin*, silver, *kyō*, apricot; cf. Thommen, 1949). Thunberg in 1776 travelled from Nagasaki to Yedo and back along the same route (cf. Stearn, 1947) as Kaempfer had done earlier.

Kaempfer was not the first German to botanize in western Asia. In 1558–60 Melchior Wieland (1520–89) made a journey to Greece, Syria and Egypt. On the return journey he had the misfortune to be captured and enslaved, though ransomed later by Gabriele Falloppio ; ultimately he became superintendent of the Padua botanic garden. His travels added nothing to current knowledge. A more important traveller was Leonhart Rauwolf (d. 1596) who, like J. Bauhin, Clusius, d'Aléchamps, l'Obel, Pena, Felix Platter, Rabelais and Sarrazin, learned botany from Rondelet (Rabelais's Rondibilis) at Montpellier and who journeyed in 1573–75 from Tripoli in Lebanon to Baghdad and Mosul and back to Tripoli, also visiting Palestine. He brought home a herbarium of 350 plants,

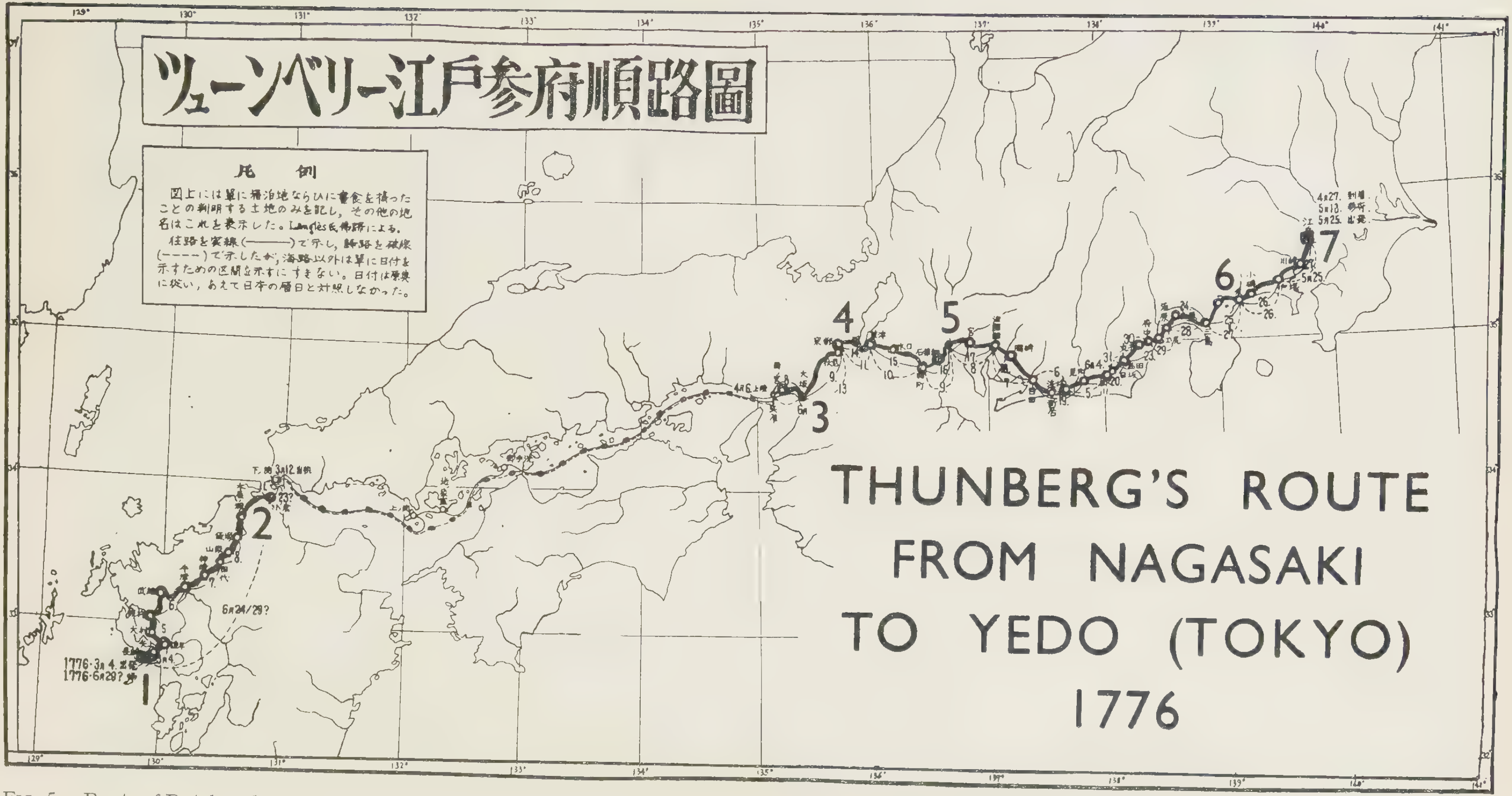
ツューンベリー江戸参府順路圖
凡例
図上には單に宿泊地ならびに晝食を摂ったことの判明する土地のみを記し，その他の地名はこれを表示した。Langlès氏翻譯による。
往路を實線（———）で示し，歸路を破線（－－－－）で示したが，海路以外は單に日付を示すための区間を示すにすぎない。日付は原典に従い，あえて日本の曆日と対照しなかった。
THUNBERG'S ROUTE
FROM NAGASAKI
TO YEDO (TOKYO)
1776
1
2
3
4
5
6
7
1776·3月4.
1776·6月29?
6月24/29?
4月6.
4月27.
5月13.
5月25.
129°
130°
131°
132°
133°
134°
135°
136°
137°
138°
139°
140°
141°

FIG. 5.—Route of Dutch embassies from Nagasaki to Yedo (cf. Stearn, 1947, 1948) :—1, Nagasaki, ; 2, Kokura ; 3, Osaka ; 4, Kyoto ; 5, Kuwana ; 6, Hakone ; 7, Tokyo.

now at Leyden, of which he illustrated 42 in his *Aigentliche Beschreibung der Raiss* (1583). Rauwolf died on active service as a military doctor in the Austrian army fighting the Turks in Hungary. French and Italians were not less busy in the Near East and Egypt. It must suffice to mention Pierre Belon (1518–64), who survived the perils of travel abroad only to be murdered in the Bois de Boulogne, and Prospero Alpino (1553–1613), author of *De Plantis Aegyptii* (1592). Probably the most important pre-Linnaean journey into the Near East was that made in 1700–02 by Joseph Pitton de Tournefort (1656–1708), Andreas Gundelsheimer (1668–1715) and the artist Claude Aubriet (*c.* 1665–1742) across northern Asia Minor to Trebizond (Trabzon), Erzurum, Tiflis, Ararat and Erivan.

His posthumous *Relation d'un Voyage du Levant* (2 vols., 1717) is important for the typification of many Linnaean names, its delicate and accurate engravings by Aubriet of new plants being often cited by Linnaeus, who made Tournefort's observations on Mount Ararat the subject of phytogeographical analysis. His route is mapped in R. Heim and others, *Tournefort* (1958).

In so rapid a survey as this, primarily concerned with the most notable of those who before 1733 provided material used by Linnaeus, it is manifestly impossible to mention all who had by then collected plants in various parts of the world. It seems fitting to conclude with Georg Everhard Rumpf (1627–1702), who died before Linnaeus was born but whose works did not come into Linnaeus's hands until the *Species Plantarum* was almost completed. He went to the East Indies in the employ of the Dutch East India Company in 1653 and settled in 1657 in Amboina. Rumpf was a kind of botanical Job ; in 1670 he became blind, in 1674 his wife and a daughter were killed when a earthquake demolished his house, in 1687 a fire destroyed his collections and drawings ; when he died in 1702, his work was unpublished ; in fact the vast *Herbarium Amboinense*, to which he had devoted 40 years, did not appear until 1741–50. Amboina is a small island but has a varied tropical flora. According to Merrill, Rumpf's work deals with about 1200 species, 930 of which can be given definite specific names and another 140 identified as to genus ; for 350 of these, Rumpf's illustrations and descriptions provide nomenclatural types. The *Herbarium Amboinense* is thus a lasting monument to his zeal, patience and indomitable tenacity in the face of misfortune. Linnaeus could never have made his own work so comprehensive and himself have earned such lasting renown without the devoted labours of men like Rumpf as a foundation.

Historical Importance of the Early Collectors

Compared with what has been achieved since, maybe the results of the work of these early field-botanists are not impressive. Thus Linnaeus, who through their work came to know some 6000 species of plants, concluded in 1753 that the total was not likely to exceed 10,000, whereas by 1807 the total of flowering plants alone listed by Persoon exceeded 25,000, and is now estimated at about 250,000 (cf. Jones. 1951). Of flowering plants from Ceylon, Hermann provided Linnaeus with about 430 of the 2300 or so now known from the island. Sloane provided him with about 800 of the 2500 or so now known from Jamaica. The reasons for these low figures from pre-Linnaean collectors are several. One is that Linnaeus was obliged to neglect no small part of their material ; many of their specimens and drawings were inaccessible or unknown to him and much of their published work through its lack of attention to floral details was not such as he could use. Another reason, a fundamental one, is that few of the early collectors penetrated into virgin floras. These men were not professional botanical travellers ; botany for them was usually subsidiary to medical, commercial or evangelical activities which kept them mostly in or near towns and villages. As Merrill (1954) has emphasized, by the time Linnaeus had established the binomial system in 1753, some 250 years of European control had existed in Ceylon, India, Malacca, Amboina, the Philippines, Macao etc., and an extensive commerce had been developed. Portuguese ships travelled backwards and forwards between Brazil, Angola, Mozambique and Portuguese possessions in the East. An important Spanish galleon route traversed the Pacific Ocean from Acapulco in Mexico, via Guam, to Manila in the Philippines. Along this and other trade routes the same economic plants were deliberately introduced and with them came a host of aggressive weeds, inadvertently transported in soil and ballast, in fodder for the livestock carried on long voyages, imperfectly cleaned seed, and so on. These weeds so quickly established themselves in open places near human habitations that the early collectors naturally accepted them as native where they found them. Thus Sir Hans Sloane wrote in 1707 that ' by Collections sent to the very Industrious and Skilful Botanist Mr. *Petiver*, others, and myself, from *Spain*, *Portugal*, *Barbary*, *Guinea* and the *East-Indies*, as well as by the *Hortus Malabaricus*, I find a great many plants common to *Spain*, *Portugal* and *Jamaica*, more common to *Jamaica* and the *East-Indies*, and most of all common to *Jamaica* and *Guinea*.' This was undoubtedly true of the lowland plants of open man-made habitats with which he was primarily concerned. The floristic links between the countries named had, however, been forged during the past 200 years by Spanish and Portuguese occupation and by the Transatlantic slave trade. Thus misled, Linnaeus assumed the tropical flora to be comparatively uniform, made little distinction between India and China, the East Indies and the West Indies, and gave little weight to the vastness of the unexplored territory. He evidently regarded the world's vegetation as divided into climatically determined zones, each one with characteristic species that had attained wide ranges within the zone through their fecundity and efficient means of dispersal but could not thrive outside it because of unsuitable climate. Hence he made little allowance for regional differentiation and endemism within these zones. ' On the Pyrenean, Swiss and Scottish mountains, on Olympus, Lebanon and Ida ', he stated in 1744, ' are found the same plants which clothe the Alps of Lapland and Greenland '.

Pondering over the economy of Nature and these phytogeographical matters and attempting to correlate them with past changes in the relation of land and sea for which the geology of Sweden provided evidence, Linnaeus came near to enunciating basic principles concerning the effect of environment upon plant distribution (cf. Cain, 1944 : 10) and to distinguishing floristic elements (cf. Braun-Blanquet, 1919). In 1737, in the preface to his *Flora Lapponica* (proleg. no. 7), and again in 1739, in his *Rön om Växters Plantering*, no. 23 (printed 1741 ; reprinted in *Skrifter af Carl von Linné* **4** : 140 ; 1908), he drew attention to the occurrence of similar plants on the mountains of Lapland, Switzerland, Wales, Mount Olympus, Monte Baldo, Mount Ararat and Spitsbergen, thereby recognizing the arctic-alpine floristic element. In 1743, in an address upon the increase of the habitable earth (*Oratio de Telluris habitabilis Incremento*, first printed in 1744 ; reprinted in 1751, 1752, 1762, 1764 and 1787 in *Amoenitates* vol. **2** ; translated into English by F. J. Brand in 1781), Linnaeus went further and put forward a diffusionist hypothesis of biogeography. He believed so completely in the account of Adam's activities as a zoological nomenclaturist given in the second chapter of *Genesis* that he made them the basis of his argument. ' If all the animals were in Paradise, which appears from Adam's giving them names, all the insects must have been inhabitants of Paradise ; therefore all the species of plants must have had stations assigned to them in this most pleasing garden. For every plant nourishes its peculiar insect, and most insects feed only on particular plants '. Moreover ' if that part of the globe occupied by land had been originally of the same extent which it is this day, it would have been difficult and almost impossible for Adam to have found every animal '. The transition from lowland species at the foot of a mountain such as Ararat, ascended and described by Tournefort, to arctic-alpine plants near its summit answered the problem as to how ' all vegetables in a small tract of land might find their proper soil and every animal its proper climate '. From this Linnaeus concluded that in the first ages of the world all lay immersed in the sea except a single island near the Equator with a very lofty mountain rising from a fertile plain. Ascending its slopes, tropical vegetation gave place to temperate vegetation and this to arctic-alpine vegetation near the region of perpetual snow. As land around Paradise island increased or rose out of the sea elsewhere, it was colonized from the appropriate region on the mountain of Paradise by plants suited to its climate. Despite Linnaeus's now untenable conclusion, his neat and logical correlation here of facts and suppositions not hitherto considered together is a notable piece of botanical scholarship, a pioneer essay in interpretative plant geography, of which, following Hofsten (1916), he may be considered the founder.

Thus the work of the early collectors provided a foundation not only for modern taxonomy but also for plant geography, even though the plants first brought to notice were in general the widespread ones, the weeds, the cultigens, the wild plants of medicinal or economic value. These are the plants which, although nowadays apt to be despised or disregarded by academic botanists, are those which matter most to humanity in general. Thanks to the efforts of the early collectors they received convenient binomials, at the very start of modern botanical nomenclature, from Linnaeus himself. Thus in commemorating the 250th anniversary of his birth and considering the background of his achievements it is fitting also to honour with remembrance the pioneers of botanical exploration who, despite danger and hardship and with no prospect of any material reward and with but little of fame, nevertheless provided him and us with the basic material of study. The allegorical frontispiece to Linnaeus's *Hortus Cliffortianus* (1738) graphically expresses his view of his relation to their activities. From Africa, Asia and America come three women, Negro, Arab, and Amerindian, bringing plants, the raw material of commerce, industry and science, to the goddess Cybele seated in a garden in Europe. At her side stands a young European god, Apollo, with features remarkably like those of Linnaeus, holding the torch of learning in his left hand and with his right hand thrusting back a shroud of darkness that threatened to envelope her majesty. This picture has a significance more profound than its designer intended. Unwittingly it symbolizes the making of the modern world.

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Acknowledgments

Fig. 2 is reproduced with slight modification from Bunbury, *Hist. Ancient Geogr.* (1879). Fig. 3 is based on Burkill's map in *J. Bombay Nat. Hist. Soc.,* **51** (1953). Pierre Turner, Kingston Grammar School, lettered and embellished Fig. 4. Fig. 5 is adapted from the map in *Forskningsmaterial rörande C. P. Thunberg* (Tokyo, 1953). The block of Fig. 1 has been lent by Messrs Sandbergs Bokhandel, Stockholm.

PROCEEDINGS OF THE GENERAL MEETING HELD ON 18 July 1957

Dr C. R. Metcalfe, Botanical Secretary, and Asst Professor H. R. Hewer, Zoological Secretary, alternately in the Chair.

The Proceedings of the Anniversary Meeting held on 24 May 1957, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last meeting :—Editor of *The Lady ;* Messrs Sandbergs, publishers, Messrs Almquist & Wiksell, publishers ; Assistant Literary Editor *Contemporary Review ;* the Rector of Imperial College ; the Swedish Medical Society ; Dr A. Holm ; Aligarh Muslim University ; Director National Museum of Wales ; Prof. A. J. E. Cave ; Dr H. C. D. de Wit ; Librarian Geol. Dept. University of Birmingham ; Prof. W. R. Taylor ; Prof. G. E. Trease ; The Crown Agents for Overseas Governments and Administrations ; Dr C. C. G. van Steenis and Mr F. Kingdon-Ward, O.B.E.

The following signed the Obligation in the Roll and Charter Book and were admitted Fellows :—David John Hambler, Ph.D. ; Prof. Ronald Darnley Gibbs ; Frederick Richard McQuown, M.A. ; Edward Stewart Maurer and Jagannath Dattagraya Kulkarni, B.Sc., B.Pharm., Ph.D.

The Chairman reported the deaths of :—James Erik Hamilton, I.S.O., Mrs. Alice Sophia Bacon and Dr Wilfred Rushton, Fellows of the Society.

The following candidates for Fellowship were balloted for and elected :—Robert P. Celarier, M.S., Ph.D., Lewis Leonard Forman, B.Sc., A.L.S., William Devigne Russell Hunter, B.Sc., Ph.D., and William David Lindsay Ride, M.A., D.Phil.

A Symposium on Biochemistry and Taxonomy was opened by Dr E. C. Bate-Smith (Visitor), Plant Phenolics as taxonomic guides. Dr C. R. Metcalfe, Sec. L.S., The occurrence of tannins and leuco-anthocyanins in about 500 species of dicotyledonous plants belonging to 175 families. Dr J. M. Rowson, F.L.S., Alkaloids and plant taxonomy. Prof. R. Darnley Gibbs, F.L.S., Biochemistry as an aid to establishing the relationships of some families of dicotyledonous plants. Dr P. R. Enslin (Visitor) and Dr S. Rehm (Visitor), The distribution and biogenesis of the cucurbitacins in relation to the Taxonomy of the Cucurbitaceae. Prof. Dr F. Hegnauer (Visitor), Some considerations about taxonomical significance of primary and secondary plant metabolites. Dr P. G. H. Gell (Visitor), Dr J. G. Hawkes, F.L.S., and Dr S. T. C. Wright (Visitor), The application of immunological methods to *Solanum* taxonomy ; and Dr R. Hill, F.R.S. (Visitor), Dye stuff plants. **[Papers printed under.]**

In a general discussion of these papers, the following took part :—

The Botanical Secretary, Zoological Secretary, Dr J. W. Fairbairn, Mr E. J. H. Corner, Dr K. R. Sporne, Mr P. R. Bell, Dr R. Melville, Prof. H. Flück, Prof. J. W. Purseglove, Mr A. H. Williams, Dr E. A. H. Roberts, Mr R. A. H. Graham, Mr J. B. Sillett, Prof. C. Rimington and Mr A. H. G. Alston ; Dr Bate-Smith, Dr Rowson, Prof. Darnley Gibbs, Dr Enslin, Prof. Hegnauer, Dr Hawkes and Dr Hill replied.

SYMPOSIUM ON BIOCHEMISTRY AND TAXONOMY

PLANT PHENOLICS AS TAXONOMIC GUIDES

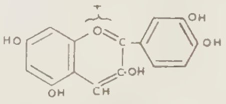
By E. C. Bate-Smith

(Low Temperature Station for Research in Biochemistry and Biophysics, University of Cambridge and Department of Scientific and Industrial Research)

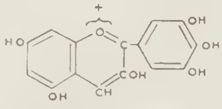
Except for the anthocyanin pigments of flower petals, little thought is given by botanists to the phenolic constituents of plants ; and this in spite of their presence in all of the higher and most of the lower plants, and the often surprising concentrations of them present in the living tissues. The reason for this lack of interest is, no doubt, that no function can, in general, be ascribed to them, and no explanation can be given for their extraordinary diversity. Both their universal presence and this very diversity suggest, however, that it would be well worth while seeking for some sign of regularity in their distribution. A search for signs of regularity is, in fact, very soon rewarded, and I am going to try to describe some of the early results of such a search.

The opportunity for these investigations arose out of a study of the phenolic constituents of the cacao bean. While some varieties of the bean contain visible anthocyanins, which impart to the cotyledons a purple colour, all varieties contain " invisible anthocyanins ", which may become visible when the beans are heated with mineral acid. Such leuco-anthocyanins, as they were called by Rosenheim (1920), were found by Robinson and his collaborators (1933, 1934) to be quite widespread in the tissues of flowering plants, and a more systematic search (Bate-Smith, 1953) showed that there was an interesting correlation between their presence in the petals and the woodiness of the plant. This was amply confirmed by a more extensive study of their systematic distribution in leaves (Bate-Smith & Lerner, 1954).

At this stage it became necessary to identify more narrowly the actual anthocyanidin pigments formed. In flowers, the anthocyanins are present as glycosides, the aglycones so far identified (i.e. the sugar-free phenolic residues) being six in number. To our surprise, we found that the leuco-anthocyanins, with exceedingly rare exceptions, produced only two types of anthocyanidins : cyanidin and delphinidin. The structural formulae of these are as follows :—



CYANIDIN



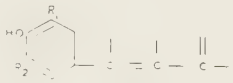
DELPHINIDIN

With the aid of paper chromatography, identification of these substances in an acid digest of plant tissues is extremely simple (Bate-Smith, 1954). At the same time, a whole series of phenolic aglycones is displayed on the paper, and a large number of these can now be confidently identified. The opportunity is thus gratuitously provided for detecting any regularity that there may be in the distribution of these constituents.

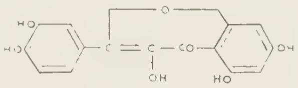
A preliminary account of these results has been published (Bate-Smith, 1956), in which details may be found of the analytical procedures.

The Commoner Phenolic Constituents.

It emerges from this survey that three classes of phenolic constituents overwhelmingly predominate in the leaves of vascular plants : leuco-anthocyanins, flavonols, and hydroxycinnamic acids. These, and also a great many of the less common plant phenolics, are closely related chemically, having in common a benzene ring carrying one, two or three hydroxyl groups and a three-carbon unsaturated side chain, e.g. :—



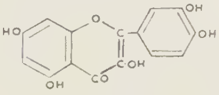
where R_1 and R_2 may be H or OH (or sometimes OCH_3). The presence of this grouping in the anthocyanidins and the flavonols can be seen more easily when they are depicted in the form (in this case quercetin):

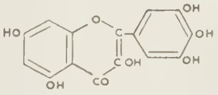


instead of the usual cyclic flavonoid configuration. We shall be especially concerned with eight of these common types, two leuco-anthocyanins, two flavonols, three cinnamic acid derivatives, and a fourth substance, ellagic acid, which, it seems, must be regarded as representing the missing trihydroxy-cinnamic acid. With this reservation, each pair of substances consists of a dihydroxy and a trihydroxy representative of its class. These are :—

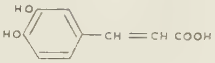
Class	*Dihydroxy*	*Trihydroxy*
Leuco-anthocyanin .	Leucocyanidin .	Leucodelphinidin
Flavonol .	Quercetin .	Myricetin
Hydroxy acid .	Caffeic acid .	Ellagic acid
Methoxy acid .	Ferulic acid .	Sinapic acid

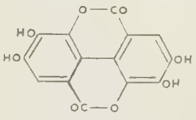
A definite structure cannot be assigned to the leuco-anthocyanins, because several different structures can satisfy their known properties. The flavonols quercetin and myricetin have the structures :—



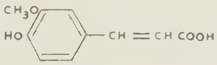


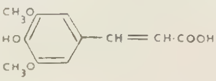
Caffeic and ellagic acids are :—





while ferulic and sinapic acids are, respectively :—

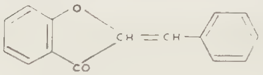




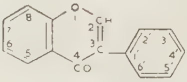
Differences are met with in the distribution of these phenolics both as regards classes, and as regards degree of hydroxyl (or methoxyl) substitution. Both the monohydroxy flavonol (kaempferol) and the monohydroxycinnamic acid (*p*-coumaric acid) are common, but they seem to be more liable to physiological variation than are the other eight common types, and to be to some extent linked, metabolically, with their dihydroxy counterparts, so for present purposes they will be left out of reckoning.

The Not-so-common Phenolic Constituents.

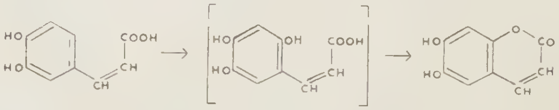
For the most part, these can be regarded as progressively less oxidized counterparts of the commoner types. Thus the catechins are less oxidized, by the equivalent of one hydroxyl group, than the leuco-anthocyanins ; the flavones, and flavanonols similarly, in relation to the flavonols, and the flavanones and chalkones still further reduced by one hydroxyl equivalent. The aurones, at the same level of oxidation as the flavones, are ring-closed to form a five-membered ring, the *iso*flavones are substituted at carbon atom 3 instead of at carbon atom 2. One important variation is the absence of a hydroxyl group on carbon atom 5—we ourselves for brevity call such compounds " 5-anoxy " compounds. They seem likely to be particularly useful in systematic diagnosis, since they are, as a class, brilliantly fluorescent. Occasionally, as in gossypetin and quercetagetin, there is an *extra* hydroxyl group at position 8 or 6, and frequently, in the cinnamic acid series, oxidation occurs at position 2 leading, by lactone formation, to the corresponding coumarin, e.g. aesculetin from caffeic acid :—



AURONE



ISOFLAVONE



CAFFEIC ACID

AESCULETIN

Other not-so-common phenolics are derivatives of benzoquinone, naphthaquinone, anthraquinone, and xanthone.

Nitrogen-containing phenolics, such as the berberine class of alkaloids and the so-called nitrogenous anthocyanins, are restricted to closely-related groups and are therefore particularly useful as systematic indices.

Methylation of hydroxyl groups is common in the anthocyanins and (as we have seen) in the cinnamic acids, but, although exceedingly varied, it is less common in the other classes of phenolic compounds. The occurrence of particular methylated phenolic compounds can, therefore, often represent a useful taxonomic guide. This is also true, as has recently been pointed out by Simmonds & Stevens (1956), of the still rarer methylenedioxy compounds.

We have, therefore, two kinds of situations which can provide guidance in taxonomy : the first kind rests on the pattern of distribution of a small number of common phenolic constituents, and the second kind derives from the limited distribution of particular uncommon constituents. It is with the first kind that this paper is mainly concerned.

The Systematic Distribution of the Phenolic Constituents.

In work of this kind it is necessary to keep in mind at one and the same time both the essential chemistry and the essential systematics of the plants one is dealing with.

Having attempted to provide a simplified account of the chemistry of the plant phenolics, I am now going to attempt a simplification of the classification of the plants in which they occur. This might be based on any one of the better known systems of classification, and I have chosen the Engler & Prantl system solely because it appears to be the one most used, and therefore the most familiar, of the current systems.

In this system the Dicotyledons are divided into two sections, the Archichlamydeae of 30 orders and the Sympetalae of 10 orders. These orders vary greatly in size, from those with numerous, often large, families, to those of only one family, sometimes of only one genus. In the simplified arrangement I have adopted (Table VI), several sequences of orders are grouped together, because they prove to be fairly homogeneous with respect to the " characters " we are considering.

The Monocotyledons are more difficult to deal with, since the orders, and even many of the families, are not so consistent within themselves as are those of the Dicotyledons. The Monocotyledons will therefore only be dealt with very briefly, in connection with the description of a single genus, viz. *Iris*.

Distribution of the Phenolic Constituents in the Leaves of Dicotyledons.

1. *Leuco-anthocyanins.*—These, as may be seen in Table I, are for the most part absent from the Centrospermae, the Umbelliflorae, and the Contortae, entirely absent from the Rhoeadales, the Tubiflorae, the Plantaginales, the Cucurbitales, and (except for two isolated species) the Campanulatae, and

TABLE I.—Families without, or (in brackets) having numerous members without, leuco-anthocyanins in the leaves.

Piperales	Piperaceae
Garryales	Garryaceae
Urticales	(Moraceae)
Santalales	(Santalaceae)
Aristolochiales	Aristolochiaceae
Centrospermae	(Aizoaceae)
	Amaranthaceae
	Basellaceae
	Caryophyllaceae
	Chenopodiaceae
	(Nyctaginaceae)
	Phytolaccaceae
	(Portulacaceae)
Ranales	(Berberidaceae)
	Calycanthaceae
	Cneoraceae
	Hernandiaceae
	(Lardizabalaceae)
	Monimiaceae
	Ranunculaceae
Rhoeadales	Capparidaceae
	Cruciferae
	Moringaceae
	Papaveraceae
	Resedaceae
Rosales	(Leguminosae-Papilionatae)
Geraniales	(Euphorbiaceae)
	Geraniaceae
	Linaceae
	(Rutaceae)
	Simarubaceae
	Tremandraceae
	Tropaeolaceae
	Zygophyllaceae
Sapindales	Aquifoliaceae
	Buxaceae
	Corynocarpaceae
Malvales	(Malvaceae)
Parietales	Caricaceae
	Datiscaceae
	(Flacourtiaceae)
	Loasaceae
	Passifloraceae
	Turneraceae
	Violaceae
Opuntiales	Cactaceae
Myrtiflorae	(Combretaceae)
	(Elaeagnaceae)
	Hippuridaceae
	Lecythidaceae
	Lythraceae
	Nyssaceae
	Onagraceae
	(Pittosporaceae)
	Punicaceae
	Thymelaeaceae
Umbelliflorae	Araliaceae
	(Cornaceae)
	Umbelliferae
Primulales	(Myrsinaceae)
Contortae Tubiflorae Plantaginales Cucurbitales Campanulatae	All except (Apocynaceae) (Asclepiadaceae) (Polemoniaceae)
Rubiales	Valerianaceae
	Dipsacaceae

absent from many families in the Ranales. The Rosales, Sapindales, and Malvales each contain numerous members in particular families or sections of families (such as Leguminosae-Papilionatae) which are negative for leuco-anthocyanins. In the Geraniales and Parietales there are also many such members, but with less well-defined relationships. The remaining orders all consistently contain leuco-anthocyanins. By and large, these are orders of woody plants. It is in fact very noticeable, as has been pointed out on several previous occasions (Bate-Smith, 1953, 1956; Bate-Smith & Lerner, 1954; Bate-Smith & Metcalfe, 1957), how closely correlated is the presence of leuco-anthocyanins in the leaves with woody habit in the plant. It is, however, remarkable how few of the woody plants in the last six orders of the Sympetalae contain leuco-anthocyanins. These are found only in the Apocynaceae, Asclepiadaceae, Rubiaceae, and Caprifoliaceae, while the quite considerable trees in the Oleaceae, Verbenaceae, Scrophulariaceae and Bignoniaceae contain no leuco-anthocyanins whatever. Conversely, the herbaceous Primulaceae and Plumbaginaceae (also placed in the Sympetalae) are rich in leuco-anthocyanins. It is clear, therefore, that there are considerations both of systematic position and of habit that determine the distribution of these constituents*.

The most striking example of the interaction of the two factors of systematic relationship and habit is provided by the Leguminosae-Papilionatae. This subfamily, by contrast with the Mimosoideae and Caesalpinioideae, is mainly herbaceous, but in it there are a number of well-known trees such as *Robinia pseudacacia* L. and *Sophora japonica* L. The trees and herbs in the subfamily are divided fairly equally as to those whose leaves do, and those whose leaves do not, contain leuco-anthocyanin, and this division is readily seen to follow more or less the accepted division into tribes. The agreement falls down, however, in a number of instances, and this was unexplained until Dormer's (1946) work came to notice. Dormer found that the presence or absence of a foliar pulvinus, which in general divided the tribes of the Papilionatae into two groups, was not a constant character in the Galegeae and the Hedysareae, and it was in just these two tribes that the irregularity in distribution of leuco-anthocyanins occurred. On further examination, it appeared that the two characters coincided in their incidence to a remarkable degree. Table II is taken from Table I in Dormer's paper and shows the division into pulvinate and epulvinate tribes, with occasional specific exceptions; and, in the case of the Galegeae and Hedysareae, into pulvinate and epulvinate subtribes. Against each division is recorded the presence or absence of leuco-anthocyanins in the leaves of members of the division so far as at present known. (In the case of *Abrus* presence in the leaves is presumed from a positive reaction for tannin in the stem; cf. Bate-Smith & Metcalfe, 1957). Only two notable discrepancies remain: a negative reaction in *Sophora* spp., and strong positive reactions in the Euhedysarinae (*Hedysarum* and *Onobrychis*).

The coincidence of the presence of foliar pulvini and leuco-anthocyanins in the same plant has a physiological explanation in the association between motility and tannin matter in the contractile vacuoles of the pulvinar cells (cf. Datta, 1957). Both foliar pulvini and leuco-anthocyanins are constantly present in the Mimosoideae and Caesalpinioideae, the former of which provides the best-known example of foliar movement.

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* Gibbs (*Proc. Roy. Soc. Canada*, 1954, **48**, (V), 1; this vol. p. 216) has described the results obtained when the wood of numerous species of plants is allowed to stand up to 24 hours with cold methanolic HCl. In many instances a purple or magenta colour is produced. The species giving positive results agree closely with those having leuco-anthocyanins in the leaves. It seems probable that the cold methanolic HCl reaction is due to leuco-anthocyanins in the wood, the blueness of the colour being due in part to the different conditions of the test and in part to the different molecular state of the leuco-anthocyanins in the wood.

TABLE II.—Coincidence of foliar pulvinus and leuco-anthocyanins in tribes and subtribes of the Leguminosae-Papilionatae.

Pulvinus present		Pulvinus absent	
Tribes			
Sophoreae	+ and −	Trifolieae	(+) and −
Dalbergieae	+	Loteae	−
Phaseoleae	+ and −	Podalyrieae	−
Abrus	+	Vicieae (except *Abrus*)	−
Subtribes of Galegeae			
Glycyrrhiza	++	Astragalinae (except *Glycyrrhiza*)	−
Tephrosiinae (except *Galega*)	+	*Galega*	−
Robiniinae	++	Coluteinae	(+) and −
Psoraliinae	+		
Subtribes of Hedysareae			
Desmodiinae	++	Coronillinae	+ and −
Stylosanthinae	(+)	Euhedysarinae	++
Aeschynomeninae	(+)		

2. *Flavonols.*—Even more than in the case of the leuco-anthocyanins, it is the absence rather than the presence of flavonols that is of significance in systematics, because they are so widespread.

TABLE III.—Families without, or (in brackets) having numerous members without, flavonols in the leaves.

Piperales	Piperaceae	Contortae	(Gentianaceae)
Centrospermae	(Aizoaceae)		Loganiaceae
	(Basellaceae)	Tubiflorae	Acanthaceae
	(Phytolaccaceae)		(Bignoniaceae)
Ranales	(Eupomatiaceae)		Gesneriaceae
	(Menispermaceae)		Globulariaceae
Rosales	(Leguminosae)		Labiatae
Geraniales	Linaceae		Lentibulariaceae
	(Oxalidaceae)		Myoporaceae
Malvales	(Malvaceae)		Orobanchaceae
Parietales	(Caricaceae)		Scrophulariaceae
	(Flacourtiaceae)		Verbenaceae
	(Ochnaceae)	Plantaginales	Plantaginaceae
	Passifloraceae	Rubiales	Dipsacaceae
	(Turneraceae)	Campanulatae	Campanulaceae
			Compositae
			(Stylidiaceae)

It will be remarked (cf. also Table VI) to what an extent the families in Table III agree with those in Table I. Here again the Centrospermae, Ranales, Geraniales, Parietales, Rosales (Leguminosae only) and the last five orders of Sympetalae are represented. Of the sympetalous families, it is those with regular flowers which are absent and those with zygomorphic flowers which are present in Table III, and this, considering also such families as the Leguminosae, may perhaps give a clue to the morphological character with which the absence of flavonols might be linked.

3. *The hydroxy acids.*—Here again, the families in which these phenolic constituents are present are far more numerous than those from which they are absent, or largely absent. Table IV therefore lists their distribution in a negative sense, the families in brackets being those in which the hydroxy acids are occasionally present.

Table IV.—Families without, or (in brackets) having numerous members without, hydroxy-acids in the leaves.

Urticales	(Moraceae)	Sapindales	(Balsaminaceae)
Proteales	Proteaceae		(Buxaceae)
Centrospermae	Aizoaceae	Rhamnales	Rhamnaceae
	(Basellaceae)	Parietales	Begoniaceae
	Caryophyllaceae		Passifloraceae
	(Chenopodiaceae)		Violaceae
	Phytolaccaceae	Opuntiales	Cactaceae
Ranales	(Lauraceae)	Myrtiflorae	Thymelaeaceae
	(Calycanthaceae)	Primulales	Myrsinaceae
	Myristicaceae		(Primulaceae)
	(Ranunculaceae)	Plumbaginales	(Plumbaginaceae)
Rhoeadales	Cruciferae	Ebenales	Ebenaceae
Rosales	Crassulaceae	Contortae	Gentianaceae-Gentianoideae
	(Leguminosae)		
Geraniales	(Cneoraceae)	Tubiflorae	Polemoniaceae
	Tremandraceae	Campanulatae	(Campanulaceae-Lobelioideae)
	(Rutaceae)		
	(Oxalidaceae)		
	Linaceae		

In this table, once again, the Centrospermae are prominent, Ranales, Rhoeadales, Geraniales, and Parietales are represented, and all three subfamilies of Leguminosae are included, but the last five orders of Sympetalae are represented only by Polemoniaceae and Campanulaceae-Lobelioideae.

The Umbelliflorae are absent from these lists. The Primulales, Ebenales, Urticales (Moraceae), Proteales, and Crassulaceae in Rosales appear for the first time. All these families have their own particular biochemical features.

4. *The methoxy acids.*—In Dicotyledons, ferulic and sinapic acids are more frequently absent than present, so that in their case it is more instructive to list

Table V.—Families in which the methoxy-acids are present.

Piperales	(Piperaceae)	Malvales	Malvaceae
Urticales	(Ulmaceae)	Parietales	Flacourtiaceae
Santalales	(Santalaceae)		Turneraceae
Aristolochiales	(Aristolochiaceae)	Opuntiales	Cactaceae
Centrospermae	(Aizoaceae)	Myrtiflorae	Elaeagnaceae
	Amaranthaceae	Umbelliflorae	(Araliaceae)
	Basellaceae		(Cornaceae)
	Caryophyllaceae		(Umbelliferae)
	Chenopodiaceae	Ebenales	Styracaceae
	Nyctaginaceae	Contortae	(Apocynaceae)
	Phytolaccaceae		Asclepiadaceae
	Portulacaceae		Loganiaceae
Ranales	Berberidaceae		(Oleaceae)
	(Calycanthaceae)	Tubiflorae	(Acanthaceae)
	Lardizabalaceae		(Bignoniaceae)
	Monimiaceae		(Boraginaceae)
	(Magnoliaceae)		Globulariaceae
	(Ranunculaceae)		Hydrophyllaceae
	(Trochodendraceae)		(Labiatae)
Rhoeadales	Capparidaceae		(Martyniaceae)
	Cruciferae		(Polemoniaceae)
	Papaveraceae		(Scrophulariaceae)
Rosales	(Leguminosae-Papilionatae)		Solanaceae
			(Verbenaceae)
	Pittosporaceae	Rubiales	(Dipsacaceae)
Geraniales	(Cneoraceae)		(Rubiaceae)
	(Euphorbiaceae)		
	(Meliaceae)		Valerianaceae
	Polygalaceae	Cucurbitales	(Cucurbitaceae)
	(Rutaceae)	Campanales	(Campanulaceae)
Sapindales	Buxaceae		(Compositae)
	(Corynocarpaceae)		

their occurrence in a positive, rather than a negative, sense. Following the convention adopted in the previous sections, the families in brackets are those in which numerous, but not all, members examined contained the methoxy acids.

The correspondence between the families in Table V and those in Table I, especially, is immediately striking. Table I, however, contains about 23 more families than are listed in Table V. These on further inspection prove to belong for the most part to the Geraniales, and the Parietales, and (as will in due course appear) in many cases possess ellagic acid. By and large, there is a remarkable correlation between the presence of " tannins " and the presence of the methoxy acids. This is not the time and place to discuss the possible reasons for this, but it may be pointed out that the presence of leuco-anthocyanins is correlated with woodiness, and that in their chemical structure, ferulic and sinapic acids are closely allied to the unit residues from which lignin is thought to be synthesized.

5. *Restricted and specific constituents.*—Professor Hegnauer (1956) has pointed out that particular value as systematic guides attaches to uncommon constituents whose distribution is limited to particular groups. We have seen that some guidance is to be obtained from the *absence* of the very common constituents, and from the *presence* of some of the less common ones. Substances of unique occurrence are virtually, by definition, useless as systematic guides. Especial usefulness is met with in such distinctive classes as the anthraquinones, the " nitrogenous anthocyanins ", and the *iso*flavones. In the middle range are substances which are neither common nor restricted in distribution, which are not very easily identified, and whose distribution has not yet, in consequence, been very extensively mapped. Substances of this kind are the flavones, the flavanones, the catechins, and the coumarins.

The distribution of some of the uncommon and restricted classes of phenolics, and of some particular individual constituents, is shown in Table VI. Particular value as systematic guides attaches to the " nitrogenous anthocyanins ", since these, while consistently present in all members of the Centrospermae (with the exception of the Caryophyllaceae) are also found in the Cactaceae, confirming the systematic position of this family in or near the Centrospermae. We are inhibited in any attempt to interpret these observations from a lack of present knowledge of the composition of these substances.

The protopine and berberine alkaloids are similarly restricted to the Ranales and Rhoeadales, except for one isolated family in another order, viz. the Rutaceae in Geraniales.

Anthraquinones have been reported in a rather wider range of families, but not always with certain identification. They are especially associated with the Polygonaceae, the Rhamnaceae and the Rubiaceae, and can be taken as a biochemical characteristic of these families. They also occur in *Aloe* in the Monocotyledons.

*iso*Flavones are restricted in an interesting way to three families, each of the families having different types of *iso*flavones. Those in the Leguminosae and Rosaceae are similar in their basic hydroxylation pattern, but differ in respect of the position of methylation. Elsewhere *iso*flavones have only been reported in the genus *Iris* in the Monocotyledons, and the types there present are widely different from those in the two dicotyledonous families.

One other class of substances which could have interesting possibilities as indicators of relationship might be mentioned. These are the dihydrochalkones, of which phloridzin is the best-known representative. This has been reported in many species of *Malus* in the Rosaceae, in *Kalmia* and *Pieris* in the Ericaceae, and in *Micromelum tephrocarpum* Turcz. in the Rutaceae. There is another biochemical link between the Rosaceae and the Ericaceae in arbutin, a glucoside of hydroquinone which occurs in *Pyrus* species, in which phloridzin is not found, and in many ericaceous plants.

TABLE VI.

	Archichlamydeae												Sympetalae				
E.P. orders	1-16	Centro-sperm. Cact. 17 & 28	Ran. Rhoead. 18–19	Sarrac. 20	Rosal. 21	Geran. 23	Sapind. 24	Rhamn. 25	Malv. 26	Pariet. 27	Myr-tif. 29	Um-bell. 30	Eric. 1	Prim. Plumb. 2 & 3	Eben. 4	Con-tort. 5	6-10
Leuco-anthocyanins	+	[illegible]	(+) −	+	+	[illegible]	+ (−)	+	+ −	+ −	−	−	+	+	+ −	−	(+) −
Flavonols	+	+ (−)	+	+	+ (−)	+	+	+	+	+ (−)	+	+	+	+	+	+	+ −
Hydroxy acids	+ (−)	−	+ −	+	+ (−)	+ (−)	+ −	+ (−)	+	+ (−)	+	+	+	−	+ −	+	+
Methoxy acids	(+) −	− +	+		(+) −	(+) −	(+)	−	−	(+)	(+) −	+	−	−	(+) −	+	+ +
Ellagic acid	+	−	(+) −	+ −	+	+	+	+	−	+ −	+	(+) −	+	−	−	−	−
Nitrogenous anthocyanins	−	+ +	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Anthraquinones	+ Polygonaceae	−	−	−	+ ? Leguminosae	+ Rutaceae	−	+ +	−	−	−	−	−	?	−	−	+ Rubiaceae Verbenaceae
Berberine alkaloids	−	−	+ +	−	−	+ Rutaceae	−	−	−	−		−	−	−	−	−	−
*iso*Flavones	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−

TABLE VII.—Distribution of Phenolics in Tribes of Rosaceae.

	Spiraeoideae		Pomoideae	Rosoideae							Prunoideae	Chryso-balanoideae	
					Potentilleae								
	Spiraeeae	Quillajeae (*Exochorda*)	Pomarieae	Kerrieae	Rubinae	Potentillinae	Dryadinae	Ulmarieae	Sanguisorbeae	Roseae	Pruneae	Chrysobalaninae	Hirtellinae (*Parinarium*)
Leuco-anthocyanins	++	+	++	+−	+−	+	−	(+)	++	−	+	LCy − LD +	LCy + LD −
Flavonols	++	++	++	(+)	++	++	−	++	++	++	++	Q + M ++	Q + M −
Caffeic acid	+	− ?	++	−	+	+	+	+	+	+	++	+−	−
Ellagic acid	−	−	−	−	+	+	+	+	+	+	−	−	−
Ferulic acid	+−	−	−	−		+	−	−		+−	(+) −	−	−

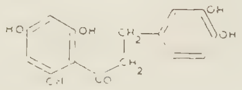
These are, of course, but a few examples from many that might be quoted of the restricted occurrence of particular classes of phenolic constituents. The systematic relationships that they suggest may be real, or they may—and often must—be accidental. Furthermore, up to the present we have considered the occurrence of the commoner constituents in leaves only, and there are already indications that the study of other tissues would prove just as informative from the systematic point of view. A great deal of attention has been paid, for instance, to the phenolic constituents of wood, especially that of conifers by Erdtman and that of *Prunus* species by Japanese workers. With P. Ribéreau-Gayon I have recently carried out a limited chromatographic survey of the phenolic constituents of seeds. In most instances the results have agreed with those obtained with the leaves of the same species, but there was one striking exception : the seeds of the Leguminosae proved to contain leuco-anthocyanins, whether or not these were present in the leaves of the same species. Their absence from the leaves of the epulvinate tribes of the Papilionatae is therefore to be interpreted as the local suppression of a synthetic capacity originally possessed by its whole plant. This is not the case, however, in such families as Chenopodiaceae, Campanulaceae, or Scrophulariaceae, where so far no part of the plant has been found to contain leuco-anthocyanins. By extending our survey to tissues other than leaves it may, therefore, be possible to establish even more clear-cut distinctions on biochemical grounds than those which have already been discerned.

Distinction between Different Tribes within a Family.

As an example of the extent to which the phenolic constituents agree with the subdivision of a family based on exomorphic characters, the Rosaceae may be selected for discussion. This family is distinctive for the rarity of occurrence of trihydroxy-substituted constituents in it, but such as do occur are confined to very distinct tribes. Other tribes, and some genera, have their own distinctive and in some cases unique constituents.

The overall pattern is that of a generally woody family, many of the members being shrubs, some canes or briars, some herbaceous. The leaves, especially of the woody members, are rich in flavonols (quercetin and/or kaempferol, but not, however, myricetin) and leuco-anthocyanins (leucocyanidin, not leucodelphinidin) ; the only exceptions to this rule among 120 species examined being *Chrysobalnus pelloacarpus* G. F. W. Mey. *Licania rigida* Benth. and *Potentilla anserina* L., which contain myricetin and leuco delphinidin as well as quercetin and leucocyanidin. The herbs and briars in the Rosoideae often contain no leuco-anthocyanins, and sometimes contain no flavonols, or no chlorogenic acid, but the Rosoideae, and the Rosoideae *only*, consistently contain ellagic acid, Ferulic acid is sometimes present, but as would be expected of a generally woody family, is generally absent.

As regards specific constituents, mention has already been made of the presence of phloridzin in *Prunus* and *Malus* species and of arbutin in the genus *Pyrus*. A glucoside of the corresponding dihydroxy compound to phloretin has been found (Williams, 1956) in four only of 25 species of *Malus*, and these are all members of the Sieboldianae (Rehd.). There is a highly significant correspondence between the distribution of the heartwood constituents in the genus *Prunus* and the systematic divisions of this genus.



Distinctions between the Different Sections of a Genus.

The genus *Iris* affords an opportunity not only of examining the way in which differences between species of a single genus reflect the morphological differences on which the division of the genus has been based, but also the situation in Monocotyledons generally. Table VIII gives the results which have been obtained for members of seven of the twelve sections into which the genus is divided by Dykes (1913), one of these, the Apogon section, being further divided into eight subsections and a miscellaneous group.

TABLE VIII.—Distribution of Phenolics in Sections of *Iris*.

				Apogon										
	Reticulata	Juno	Pardanthopsis	Sibirica	Spuria	Californica	Hexagona	Laevigata (*Pseudacorus*)	Foetidissima	Unguicularis	Ensata	Regelia	Evansia	Pogoniris
Leuco-anthocyanins	—	—	—	+	+	+	—	+	—	—	—	+		—
Flavonols	—	—	—	+	—	—	—	—	—	—		—		—
Caffeic acid	—	—	—	+ —	(+)—	+	+	—	(+)	(+)	—	+	—	—
Methoxy-acids	?	+	+	+	+	+	+	—	+	+	+	+	+	—
*iso*Flavones (rhizome)	—	—	—	—	—	—	—	—	—	—	—	—		—

In general, the universal presence of the methoxy acids is to be noted. Next, the biochemical similarity between the Evansia and Pogoniris sections, regarded as equivalent eastern and western groups, respectively. Third, the co-occurrence of leuco-anthocyanins with flavonols and caffeic acid and the virtual restriction of these to the one (Apogon) section. As a point of especial interest, the position of the species *I. flavissima* Palt. included in the Pogoniris section by Dykes, was questioned by Simonet on the grounds of its anomalous chromosome number, and its placing is equally to be doubted on biochemical grounds. Its phenolic constitution would agree with its inclusion in the Regelia section, the position preferred by Simonet, and now adopted by the Iris Society.

The biochemical variation within the genus is considerable, but no more so than the variation in such important respects as the bulbous and rhizomatous nature of the root system. There is no distinction here as between woody and herbaceous forms, and this is quite general in the Monocotyledons. In this class the herbaceous habit is so predominant that distinctions other than those associated with the woody and herbaceous habit come more clearly into evidence. One such distinction is that between aquatic or marshy as opposed to the terrestrial habitat. In the genus *Iris*, for instance, it is in the leaves of the moisture-loving species in the Apogon section that leuco-anthocyanins are found, and this appears to be fairly general for the Monocotyledons as a whole.

Such distinct families as the Gramineae and the Palmae are biochemically very constant. In the Gramineae the main phenolic constituents are ferulic acid and flavones; leuco-anthocyanins, flavonols, and caffeic acid being rarely present. The supposedly nearly related Cyperaceae, however, constantly contain flavonols and leuco-anthocyanins. The woody Palmae follow the rule in having leuco-anthocyanins, caffeic acid, and often flavonols, but surprisingly the Musaceae and the Zingiberaceae also have these constituents (kaempferol is, in fact, named as a result of its isolation from one of the latter family). It is interesting to note that ellagic acid has only once been reported in the Monocotyledons, namely from *Hypoxis filiformis* Baker—a result so isolated that it calls for confirmation if and when the opportunity occurs.

Reasons for Regarding the Phenolic Constituents as a Biochemically Privileged Class.

The first reason for taking this view is that the phenolic compounds appear to be metabolically inert. They are formed in the living cell in considerable amounts, and nothing, so far as is known, happens to them in the living cell but to be laid down in the cell-wall. The phenolic compounds found in the living tissues are, therefore, stable and characteristic end-products.

The second reason is that the chain of biosynthetic processes leading to their formation appears to be irreversible from the point where quinic acid (which, it will be remembered, is richly present in combination with the hydroxy-aromatic acids) is converted through shikimic acid to the first true aromatic residue. There seems to be a narrow channel into a closed area of biosynthesis from which the only escape route is total oxidation.

Within this area, however, the forms assumed by the end-products of synthesis can be many and various. Usually the forms found in the less woody plants differ from those in the more woody ones by being less oxidized: flavones. aurones and chalkones rather than flavonols; or more methylated: methoxy acids rather than hydroxy acids. The extent of such differences is, however, rigidly defined for the species, so that the phenolic compounds present in the tissues are characteristic of the species, and are often shared by species of the same genus or family. These conclusions pose significant questions for the physiologist both as regards the mechanism of the synthetic processes at work in the plant-cell and as regards the function of the phenolic constituents in the life of the plant. Answers to these questions must be important to the taxonomist because they will go a long way towards supplying the *reasons* for the morphological differences on which his systems of classification are based. In the meantime, there are already a number of guides to classification in the precise array of phenolic substances which a plant is able to fabricate, and which the biochemist can now so easily identify.

SUMMARY.

The distribution of leuco-anthocyanins, flavonols, and certain aromatic acids in the leaves of flowering plants is discussed in relation on the one hand to the Englerian system of classification and on the other hand to the woody or herbaceous habit of the plant. Broadly, leuco-anthocyanins are present in the members of woody families, and the methoxycinnamic acids in herbaceous plants. While the flavonols and hydroxy-acids are generally present, many of the families from which they are absent are regarded as closely related in this system,

or have certain morphological characters in common. In the Leguminosae-Papilionatae, the presence of leuco-anthocyanins in the leaves is closely correlated with the presence of foliar pulvini. In the Rosaceae, ellagic acid is present only in the tribe Rosoideae. In the genus *Iris*, the phenolic constituents closely follow the sectional division of the genus. Anthraquinones, nitrogenous anthocyanins, *iso*flavones, the berberine alkaloids, and phloridzin are restricted in their distribution mainly to groups of closely related plants. The phenolic constituents thus appear to offer opportunities for guidance in detecting relationships between plants and groups of plants.

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THE OCCURRENCE OF TANNINS AND LEUCO-ANTHOCYANINS IN DICOTYLEDONOUS PLANTS

By C. R. METCALFE, Sec. L.S.

THE occurrence of tannins and leuco-anthocyanins in about 500 species of dicotyledonous plants belonging to 175 families was discussed from the taxonomic and phylogenetic standpoints. This contribution formed a supplement to the one from Dr E. C. Bate-Smith, in collaboration with whom the subject was investigated. **[A full account is printed in** *Journal, Botany,* **No. 362.]**

ALKALOIDS AND PLANT TAXONOMY

By J. M. Rowson

Alkaloids are not readily and precisely defined, but they may be regarded as relatively complex organic bases occurring naturally in plants and usually possessing marked pharmacological activity. Their basicity is due to the presence of one or more nitrogen atoms which may exist as primary or secondary amines or as cyclic compounds which may be tertiary or quaternary.

Alkaloids show many physical and chemical properties in common and are readily identified. Despite these common properties they differ widely in chemical structure, and the chemist classifies them according to the type of nucleus present in the molecule. Admittedly, some of the complex alkaloids may be classified in more than one group and in any case the nuclear structure is arrived at only after drastic degradation reactions. Also the properties of the alkaloids are determined very largely by the additional groups present rather than by the nucleus itself.

The chemists find this system of classification adequate for their purposes but it should not automatically be expected that it exhibits the natural affinities of the plants producing the alkaloids. Neither a strict chemical arrangement nor a purely botanical classification appear to fully classify all the facts of alkaloid biochemistry.

The following are examples of chemical classification according to nuclear structure of alkaloids :

A. Simple Amines, Ephedrine
B. Derivatives of Pyrrole, Nicotine.
C. Derivatives of Pyridine, Coniine.
D. Derivatives of condensed Pyrrolidine, Hyoscyamine, Cocaine.
F. Derivatives of Isoquinoline, Papaverine, Berberine.

The role of alkaloids in plant physiology is little understood. Their method of synthesis in the plant has been investigated for only a few examples—and the biogenetic pathways are little known. Since by far the greater number of plants are devoid of alkaloids these metabolites are obviously not essential for all plant life. Moreover, in recent years we have been able to produce by grafting techniques plants free from alkaloids which normally should contain them ; or plants containing alkaloids which should be free from them, e.g. *Datura stramonium* devoid of hyoscyamine ; tomato containing 0·3 per cent hyoscyamine. In all instances the plants were as healthy as the controls. Thus, these alkaloids do not appear to be essential for the plant's metabolism where normally present, nor detrimental when abnormally present.

As a background to this paper it must be stressed emphatically that as botanists we have a very incomplete knowledge of the total distribution of alkaloids. These substances were first isolated in the early part of the 19th century. They have been largely investigated in plants of medicinal importance and their occurrence in plants of no known medicinal activity has only been studied sporadically. No real philosophical treatment of the biochemistry of alkaloids and taxonomy can be made until a much more detailed survey of their distribution in the plant kingdom has been carried out.

It should also be pointed out that much of our information is out of date. Modern methods of isolation and of characterization are more precise and accurate than old ones ; and a re-appraisal of much of our information on alkaloids from the 19th century by these methods would be desirable. One example will suffice. The Indian drug *Rauwolfia serpentina* has been known for many years and some 30 years ago was shown to contain two series of alkaloids. The recently investigated hypotensive activity of the drug was not due to either of these. The re-investigation of the drug in the present decade has isolated reserpine and several allies which are responsible for its activity. Further work has shown that reserpine is present in several other species of *Rauwolfia*, the number has gone up steadily over the last two years and is now reported to be 11 species.

Alkaloids may be found in all parts of the plant but tend to accumulate in storage organs. The locus of synthesis has only been investigated in a few examples. The root is the site of synthesis in belladonna and stramonium, also in certain *Nicotiana* species. The leaf synthesises in other *Nicotiana* species and possibly in some *Datura* species.

Three main subject headings will be taken to illustrate the relationship or lack of it between alkaloids and plant taxonomy. They will be (*a*) the distribution of characteristic alkaloids or groups of alkaloids in species or genera of plants ; (*b*) the total content of alkaloids in a species ; (*c*) the ratio of two alkaloids present in a species. The general treatment will show examples illustrating the significance of each group, followed by indications of where the method breaks down.

(*a*) *Presence or Absence of Alkaloids*

In the present state of our knowledge it may be said that certain families of plants are characterized by the absence of alkaloids. Thus, the Labiatae and the Rosaceae are devoid of alkaloids. The gymnosperms rarely contain alkaloids, although they are present in the Taxaceae.

Members of the Fungi contain alkaloids, e.g. *Claviceps*, *Amanita* ; so do certain of the Lycopodiaceae and the Equisetaceae. At one time it was believed that the monocotyledons were free from alkaloids but they have been found in 11 different monocotyledonous families including the Amaryllidaceae and the Liliaceae. Alkaloids are more widespread in the dicotyledons and especially in the Berberidaceae, Fumariaceae, Leguminosae, Loganiaceae, Menispermaceae, Papaveraceae, Ranunculaceae, Rubiaceae and Solanaceae, but there seems to be little if any correlation between the phylogenetic position of a plant and either the presence or absence of alkaloids therein, or of the chemical nature of the alkaloids when present.

It does not follow from this that any relationships between the two disciplines of taxonomy and alkaloid biochemistry are either fortuitous or artificial. We still do not know enough about plant biochemistry to be dogmatic about the " natural classification " of alkaloids. But in some instances natural groups of plants contain one or several closely related alkaloids.

Thus all members of the Papaveraceae contain alkaloids of several differing types but all belonging to the isoquinoline series and the one alkaloid protopine is common to all species so far examined. Manske has found the same facts to hold for members of the Fumariaceae and hence concludes that there is no fundamental difference between the members of the two families—a conclusion which is in opposition to the findings of Dr Hutchinson on taxonomic grounds.

Manske also finds the alkaloids present in a large number of species in the section *Eucorydalis* to be closely related, with three exceptions. These, ' *Corydalis sempervirens* ' Pers., *C. crystallina* Engelm. ex A. Gray and *C. incisa* Pers. contain no bisisoquinoline alkaloids but do contain phthalide-isoquinolines. He thus suggests that the close relationship between these three species and the other members of the section *Eucorydalis* is no more than accidental.

The Papilionaceae also form a natural group ; all members so far examined containing members of the lupinane series of alkaloids. White has made a detailed study of the genera *Cytisus* and *Genista* and divides the species into six groups depending upon the presence or absence of sparteine, lupinine, cystisine and calycotomine.

The Compositae are generally free from alkaloids, with the lone exception of the genus *Senecio* and the closely related or synonymous *Erechtites*. Most of the more than 1000 species contain alkaloids which are derivatives of the base retronescine.

The tropane group of alkaloids are of considerable medicinal importance and serve to illustrate the attractions and pitfalls of our subject. Some members of the alkaloid group hyoscyamine, hyoscine, atropine, are present in three species of *Atropa*, eight species of *Datura*, two species of *Duboisia*, four species of *Hyoscyamus*, three species of *Mandragora* and three species of *Scopolia*. The occurrence of these alkaloids in the six genera of the Solanaceae, and their absence from other families, has led to the application of the term " solanaceous alkaloids " to these members of the tropane series.

It may be noted that although two species of *Duboisia*, *D. myoporoides* R. Br. and *D. leichardtii* F. Muell. contain the hyoscyamine series of alkaloids ; a third species, *D. hopwoodii* F. Muell. contains 2·5 per cent of a liquid alkaloid, piturine, which resembles nicotine. Thus an affinity with the solanaceous genus *Nicotiana* is shown

Rather strikingly, again, the cocaine group of alkaloids are also members of the tropane series and very closely resemble those of the hyoscyamine series. The cocaine group are present in *Erythroxylum coca* Lam. and *E. truxillense* Rusby, members of the Erythroxylaceae, but are not found in any other plants. They are thus highly specific.

This high degree of specificity is shown by a number of other alkaloids of medicinal importance. Perhaps morphine is the most striking, being confined to *Papaver somniferum* L. only. Coniine is found in *Conium maculatum* L. in fool's parsley and possibly one or two other umbellifers. The emetine group of alkaloids are found in *Cephaelis ipecacuanha* (Brot) A. Rich., *C. acuminata* Karsten. and possibly in other species of the Rubiaceae. Belonging to the same family, the genera *Cinchona* and *Remijia* contain the quinine series of alkaloids which are members of the quinoline group. Eserine and its allies have as yet only been reported for *Physostigma venenosum* Balfour and *P. cylindrospermum* Holmes. fam. Leguminoseae, used for ordeal poisons in W. Africa.

Strychnine and its ally brucine are present in *Strychnos nux-vomica* L. and several other species of *Strychnos*, fam. Loganiaceae. They are indole alkaloids. Other species in this genus contain curarizing alkaloids of the isoquinoline group closely related to those present in *Chondrodenron tomentosum* Ruiz. & Pav. and possibly other species of *Chondrodendron*, fam. Menispermaceae.

Sufficient examples have been quoted to show some relationships between the presence of an alkaloid or group of alkaloids and specific, generic or family classification. But examples of chemical affinities exceeding or differing from botanical affinities have also been observed. Several famous examples are known of alkaloids which are widespread in many botanically dissimilar families. Nicotine is found in *Nicotiana* and *Duboisia* (Solanaceae), *Asclepias* (Asclepiadaceae), *Equisetum* (Equisetaceae). *Lycopodium* (Lycopodiaceae), *Sedum acre L.* (Crassulaceae) and '*Eclipta alba* Hassk.' (Compositae). Anabasine occurs in *Nicotiana glauca* R. Grah. (Solanaceae) and in *Anabasis aphylla* L. (Chenopodiaceae). Ephedrine is present in *Ephedra* spp. (Ephedraceae), in *Taxus baccata* L. (Taxaceae) and *Sida rhombifolia* L. (Malvaceae), *d*-norephedrine is " cathine " of *Catha edulis* Forsk. (Celastraceae). Berberine is probably the most widely distributed alkaloid occurring in at least 16 genera of six different familes as follows :

Ranunculaceae—four species *Coptis*, *Hydrastis canadensis* L., one species

Xanthorrhiza, one species *Thalictrum*; Berberidaceae—11 species *Berberis*, four species *Mahonia*, one species *Nandina*; Menispermaceae—one species *Archangelisia*, two species *Coscinium*; Annonaceae—one species *Coelocline*; Rutaceae—one species *Evodia*, one species *Phellodendron*, one species *Toddalia*, one species *Zanthoxylum*; Papaveraceae—two species *Argemone*, one species *Chelidonium*, two species *Corydalis*. The caffeine alkaloids are equally widespread, being found in members of many different genera of plants.

These facts naturally raise doubts as to the significance of alkaloids in any system of plant taxonomy.

(b) *Total Alkaloidal Content*

For medicinal use it is necessary to administer alkaloids or their parent plant material in accurately controlled doses. Hence the percentage content of alkaloids in drugs has been studied consistently over many years. The external factors of season, climate, soil and environment do influence percentage content of alkaloids within certain limits. Such values can be raised within these limits by suitable cultivation methods, e.g. belladonna leaf 0·4–0·8 per cent, stramonium leaf 0·2–0·5 per cent, *Hyoscyamus niger* L. leaf 0·05–0·08 per cent.

But within such limits the quantitative alkaloidal content is a definite character of the plant species. Note in the example already quoted belladonna, $>$ stramonium, $\gg$ *Hyoscyamus niger*. To which, for striking comparison, may be added *Hyoscyamus muticus* L. which contains up to 1 per cent of the same alkaloids.

Some selection and breeding experiments have been undertaken in an attempt to isolate particularly high yielding strains. Prof. Flück has isolated one strain of *Datura stramonium* L. which consistently yields up to 0·9 per cent of alkaloids. I and other workers have shown that polyploids in the genera *Atropa*, *Datura*, and *Hyoscyamus* are richer in total alkaloids than corresponding diploid controls.

The growing consensus of evidence is that where alkaloids are present in a plant, they are in nature and amounts controlled by heritable factors.

(c) *Proportionality of Alkaloid Components*

We have already noted that alkaloids generally occur in groups, usually of similar chemical structure, rather than as single entities. In a number of plants the ratio of one constituent to either total alkaloids or to a second alkaloid present is a relatively fixed constant for the species. Thus the ratio of hyoscine to hyoscyamine in belladonna, or *Datura stramonium* is low since hyoscine comprises only 8 per cent and 15–20 per cent of total alkaloid respectively. In *Datura innoxia* Miller the ratio is high, since in this species hyoscine is the dominant alkaloid.

Similar constancy is exhibited by the ratio quinine and cinchonidine to total alkaloids in a number of *Cinchona* species. Also the ratio of emetine and other non-phenolic alkaloids to total alkaloids is higher in *Cephaelis ipecacuanha* Rich. than in *C. acuminata*.

Examples may also be quoted in which these ratios are not constant. Thus, Hegnauer and others have shown that in young leaves of belladonna and of *Datura stramonium* hyoscine is the dominant alkaloid but in the mature plant it becomes a minor component. A number of Australian workers have found considerable variation in the hyoscine to hyoscyamine ratio in *Duboisia* species and it is as yet uncertain if this is due to environment, season or age of plant. It is also a well-known fact that the morphine content of opium is not a fixed proportion of total alkaloids. Reserpine appears to comprise about 10 per cent of the total alkaloids present in *Rauwolfia serpentina* Benth., but there is some suggestion that the value is not always constant.

(d) *Conclusion*

We have seen that in a number of instances the presence or absence of an alkaloid or group of closely related alkaloids is a character that is peculiar to a plant species, genus or family. The total alkaloid content, or the proportions in which they are present is also sometimes of taxonomic significance for species. These facts suggest that the occurrence of alkaloids is of taxonomic significance although only to a limited extent.

Conversely the occurrence of the same alkaloids in groups of plants that are widely separated taxonomically, and the fact that mixed alkaloids are not always present in the same proportion in any one species shows clearly that great care is necessary in assessing their taxonomic significance.

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BIOCHEMISTRY AS AN AID TO ESTABLISHING THE RELATIONSHIPS OF SOME FAMILIES OF DICOTYLEDONOUS PLANTS

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MY interest in comparative chemistry as applied to the solution of problems in taxonomy dates back to a reading of Hutchinson's stimulating two-volume work on the families of flowering plants (1926, 1934). It would be idle, however, to pretend that I have solved many of the problems raised by his classification. The work outlined in the present communication is of more recent origin. At the end of his book on the families of dicotyledons, Gundersen (1950) calls attention to several groups of families which, he says, require further study. These include :—Aquifoliaceae, Salvadoraceae, and Oleaceae ; Loganiaceae and Rubiaceae ; Theaceae, Ericaceae, and Cyrillaceae. It occurred to me that a systematic investigation of the chemistry of these families—and of others supposedly related to them—should throw some light on their taxonomy. The eight families mentioned contain between them well over 500 genera and about 10,000 species. Extending the work to related families greatly increases these numbers, and, in the pages that follow, I am dealing with 23 families containing nearly 1300 genera and about 21,500 species.

All of these have been studied by taxonomists to the extent that they have received names and have been assigned to one place or another in one classification or another. It is safe to say, however, that the great majority of them have never been examined for their chemistry. In a preliminary study—and this can claim to be nothing more—only very simple chemical tests can be employed. A few paragraphs must suffice to describe these tests.

(a) *The HCl/Methanol Test*

A very few years before the commencement of the present work Isenberg & Buchanan (1945) published a paper giving the results of a series of tests upon wood shavings using a mixture of 25 ml. of concentrated HCl in 1000 ml. of methanol as a reagent. When shavings are immersed in a few ml. of this mixture a magenta colour (positive) or no marked colour (negative) may result. The original paper presented evidence of the usefulness of this test but gave few details. Through the kindness of the authors I was given access to a typescript which listed 277 species belonging to 123 genera in 56 families, which had been investigated by them. Isenberg & Buchanan did not know for what they were testing—nor are we really sure of this to-day though in 1951 Adler decided that the purple or magenta colour is due to the presence of catechol tannins.

In my tests I always use fresh sapwood ground up by a cheap pencil-sharpener. A little of this is covered with the reagent and left overnight. I then record separately the colour of the liquid and the colour of the wood, though for the present I use only the wood-colour in my tables. A negative result is usually ‘ cartridge buff ’ to ‘ chamois ’ (plate XXX of Ridgway 1912), a weakly-positive reaction is often ‘ liseran purple ’, a strong reaction ‘ magenta ’ to ‘ dull magenta-purple ’ (all plate XXVI of Ridgway). These colours would be close to ‘ chrome-yellow 605/3 ’ to ‘ saffron-yellow 7/3 ’, ‘ magnolia-purple 030/2 ’, and ‘ lilac-purple 031 ’ to ‘ petunia-purple 32 ’ respectively of the British Colour Council—Royal Horticultural Society *Horticultural Colour Chart* (1938 and 1941).

(b) *A Test for Leuco-anthocyanins*

Bate-Smith (1953) defines ‘ leuco-anthocyanins ’ as ‘ . . . substances which, when heated with 2 N aq. HCl or 5 per cent ethanolic HCl produce anthocyanidins . . . ’ I test for them, following Bate-Smith & Lerner (1954) very closely, as follows :—

About 0·5 gm. of fresh leaf-tissue (from mature leaves) is chopped, covered with 5 ml. of 2 N HCl and heated in a water-bath for 20 minutes. The tube is cooled, 5 ml. of isoamyl alcohol are added and the whole shaken thoroughly. A red colour (positive) in the isoamyl layer indicates anthocyanidin formed from leuco-anthocyanins (this should be confirmed by other tests see Bate-Smith & Lerner, l.c.). A greenish colour (negative) is taken to indicate the absence of leuco-anthocyanins. I find that separation is sometimes slow and, since the colours seem to be rather stable, I allow the tubes to stand overnight and record the colours next day. A strong positive reaction is usually equivalent to ‘ spectrum red ’ to ‘ carmine ’ (plate I of Ridgway). This is close to ‘ orient-red 819/2 ’ or ‘ geranium lake 20 ’ of the Brit. Col. Council—R.H.S. Charts.

Bate-Smith & Lerner record other colours due to interfering substances and I have obtained similar results. These may make decision difficult—resulting in the ‘ doubtful ’ columns of Tables I–IV.

(c) *Presence or Absence of Raphides*

Raphides are calcium oxalate crystals of a particular type which may be observed in suitable sections. I look for them in control sections mounted in water when making the syringin (1 : 1 H_2SO_4) test as described below. The ability to store oxalate in this peculiar form is restricted to certain groups of plants and may be used as evidence of relationship, as was pointed out by Gulliver almost a century ago (1866). Because raphides are easily observed it is fairly safe to assume that if no mention is made of them in plants described by plant anatomists they are absent. I have made this assumption in compiling the figures for non-occurrence of raphides in Tables I and II.

(d) *Cyanogenetic Glycosides*

I have discussed cyanogenetic glycosides and the test I use for them in some detail in a previous paper (Gibbs, 1954, pp. 9–14). There are many cyanogenetic glycosides all yielding HCN and the evolution of HCN may not necessarily provide a clue to relationship. In brief the test involves grinding plant material with water, emulsin, and chloroform and placing the mixture in a glass-stoppered tube. Attached to the stopper is a strip of sodium picrate paper (yellow). The paper becomes reddish if HCN is evolved.

(e) *Syringin Test*

The glycoside syringin is said to give a blue colour when sections of tissues containing it are placed in 1 : 1 aqueous sulphuric acid. Many plants give other colours with this reagent, the xylem becoming green, or yellow, or red (the last being correlated almost perfectly with a positive HCl/methanol reaction). In a few cases a bright yellow colour develops in the cortex : in other plants a general blackening may occur (see Gibbs, l.c., pp. 21–22 for further discussion).

I now turn to a consideration of the families to be compared here and of the results obtained from the tests mentioned above. I have found, in brief, that the members of about half of these families are consistently negative to the HCl/methanol reagent : the others are as consistently positive. I shall discuss them, therefore, in two series. The results are summarized in Tables I and II.

A. *A HCl/Methanol Negative Series*

Gundersen (l.c.), as I pointed out above, suggests that the Aquifoliaceae, Salvadoraceae, and Oleaceae which are ' of suspected relationship ' should be ' considered, from many points of view . . . '

(a) *Aquifoliaceae.*—This is a family of perhaps four genera (*Byronia*, *Ilex*, *Nemopanthus* and *Phelline*) and 416 species. It has been placed in the Celastrales by several authors, in the Guttales by Hallier (1912), and in the Sapindales by Loesener (1942) in the second edition of *Die natürlichen Pflanzenfamilien.* As near neighbours in the Sapindales we find Cyrillaceae and Salvadoraceae.

I have had access to more than 20 spp. of *Ilex* and to the sole species of *Nemopanthus*. All are negative to the HCl/methanol reagent (one doubtful test should almost certainly be excluded). Two species of *Ilex* are negative to the test for leuco-anthocyanins, *I. verticillata* A. Gray gives a doubtful reaction, while two (according to Bate-Smith & Lerner) give weakly positive results. *Nemopanthus* gives a doubtfully positive reaction. Raphides appear to be absent from the family. Metcalfe & Chalk (1950) make no mention of them, and I myself have not seen them in *Ilex* (several species) or in *Nemopanthus*. I have found no record of HCN in the family, nor have I found it myself in *Ilex* (four spp.) or in *Nemopanthus*. Syringin (1 : 1 H_2SO_4) tests on 11 members of the family have all yielded negative results.

It seems likely, then, that the family as a whole is negative to the HCl/methanol test, is negative (or weakly positive) to the leuco-anthocyanin test, lacks raphides, does not yield HCN, does not have syringin. Other families, if related to it, might be expected to show similar characters.

(b) *Salvadoraceae.*—This little family has perhaps four genera (*Azima*, *Dobera*, *Platymitium*, and *Salvadora*) and nine species. It has often been placed near the Aquifoliaceae but has also been put in other positions (Gibbs, l.c., p. 20). Gundersen (l.c.) says that it is '. . . apparently a link between

Aquifoliaceae and Oleaceae.' Cronquist (1957) in his new outline of classification, has it in the Celastrales with Aquifoliaceae. We may expect, then, that the Salvadoraceae 'should' be negative to the HCl/methanol test, be negative or weakly positive to the test for leuco-anthocyanins, lack raphides, fail to yield HCN, lack syringin if near the Aquifoliaceae or perhaps have it if nearer to the Oleaceae (see below).

Unfortunately I have few records from this family. *Azima tetracantha* Lam. and *Salvadora persica* L. are negative to the HCl/methanol test, raphides appear to be absent from the family, and the two members mentioned do not seem to have syringin. I have no information on leuco-anthocyanins and HCN. These meagre records are at least consistent with the view that the Salvadoraceae are closely related to the Aquifoliaceae.

(c) *Oleaceae.*—This is a much larger family of 'sympetalous' plants from which the family Jasminaceae is sometimes split. I shall consider it to include *Jasminum* and its relatives. It is then a family of perhaps 22 genera and about 500 species. Most authors would link it with other sympetalous families such as Apocynaceae, Asclepiadaceae, and Gentianaceae. It has been associated with the Salvadoraceae by Rendle (1930, 1938). There is also a marked tendency to link it to Loganiaceae (see below). If it is closely related to the Salvadoraceae and Aquifoliaceae it might be expected to have much the same chemistry. What are the facts? I have subjected almost 100 species, belonging to 15 genera, to the HCl/methanol test with uniformly negative results ; 14 species belonging to seven genera appear to lack leuco-anthocyanins. True raphides are probably absent but Metcalfe & Chalk (l.c.) speak of 'small acicular or prismatic crystals' and picture 'raphides' (following Solereder) in their Fig. 207. HCN has not been found though it has been looked for in many representatives.

The Oleaceae differ from the members of our first two families in having syringin in many cases.

The results, then, are again reasonably consistent with the placing of this family near the Aquifoliaceae and Salvadoraceae.

(*d*) *Loganiaceae.*—This family, which may be considered to have about 32 genera and 800 species, is often placed in the same order as the Oleaceae. Thus we find it in the Contortae of Engler & Diels (1936), the Gentianales of Bessey (1915) and of Cronquist (l.c.), and the Loganiales of Gundersen (l.c.) and of Hutchinson (l.c.). Some authors would make separate families of *Buddleia* and its near relatives, and of *Desfontainia.*

All the members available to me—18 species of seven genera—are negative to the HCl/methanol reagent. Five species, belonging to four genera, are negative to the test for leuco-anthocyanins ; raphides appear to be completely lacking in the group ; HCN has not been found, though 12 species belonging to seven genera have been tested ; while syringin appears to be present in one, and doubtfully present in several others. These results would seem to be completely in line with the suggested relationship with the Oleaceae. I have no reason so far, on chemical grounds, to exclude *Buddleia* and *Desfontainia* from the family.

(e) *The 'Woody Boraginaceae'* (*Ehretiaceae, Cordiaceae*).—To dwellers in temperate climes the Boraginaceae are essentially herbaceous. There are, however, many tropical and subtropical plants such as *Ehretia* (40 spp.) and *Cordia* (230 spp.), which are grouped by Gürke (1893) with other woody forms as subfamilies of the Boraginaceae, or are separated to form the Ehretiaceae (Schrader, 1820 ; Lindley, 1853) and/or Cordiaceae (Dumortier, 1829 ; Lindley, 1853). Hutchinson, in his *British Flowering Plants* (1948) says :—

> 'The tribes Cordieae and Ehretieae of Boraginaceae, which are perhaps not naturally placed with the true more herbaceous Boraginaceae,

> seem to connect Verbenaceae with Loganiaceae. In my general work they will be treated as a separate family, Ehretiaceae.'

If Hutchinson is correct in this view then we should expect to find that the ' Ehretiaceae ' resemble the families considered so far and also that the Verbenaceae will be found to have a similar set of ' chemical characters '. At least eight species of four genera of the former are negative to the HCl/methanol test ; *Cordia leucosebestera* Griseb. and *C. myxa* L. have been found to be negative to the test for leuco-anthocyanins while *C. sebestena* L. gives a doubtful reaction ; four seem to lack cyanogenetic glycosides ; no raphides have been seen in the group ; at least two may have syringin. These facts are all consistent with relationship to the Loganiaceae and the other members of our negative series. I do not wish to consider the herbaceous Boraginaceae here but it is interesting to note that Pulitzer (1915) found alkannin *only* in the herbaceous members of the family, an additional reason for separation from the woody forms.

(f) *Verbenaceae*.—This is a large family of about 100 genera and 2600 species. It is most frequently associated with the Boraginaceae. Myoporaceae, Labiatae, Scrophulariaceae and other families of the Tubiflorae. I have already mentioned Hutchinson's suggestion that the Ehretiaceae (Cordiaceae, woody Boraginaceae) link the Verbenaceae to the Loganiaceae.

Following my line of argument, the members of the Verbenaceae ' should ' be negative to the HCl/methanol and leuco-anthocyanin tests, should lack raphides and cyanogenetic glycosides, and might or might not have syringin.

I have subjected 48 species belonging to 22 genera to the HCl/methanol test with uniformly negative results. Most of the members tested for leuco-anthocyanins have also yielded negative results, while three have been classed as doubtful but should probably be ranked as negative. Raphides are almost certainly absent though needle crystals occur in a few cases. I have no record of HCN in the family unless one very doubtful case should prove to be positive. The Verbenaceae, then, appear to ' fit ' into our series. We must remember, however, that this is a large family of which only a small fraction has been examined.

In my earlier report on this series (Gibbs, l.c.) the Verbenaceae was the last family that had been found to ' fit '. Its close association in many taxonomists' minds with the Bignoniaceae, Labiatae, Scrophulariaceae, and Myoporaceae has led us to consider these families, too, from the chemical viewpoint.

(g) *Bignoniaceae*.—This is a family of moderate size with perhaps 110 genera containing some 750 species, many of them woody. It was included by Bessey (l.c.) in the Scrophulariales, with Scrophulariaceae and eight other families. Cronquist (l.c.) also includes it in an order of this name. Hutchinson (1926) has an order Personales which includes both Scrophulariaceae and Bignoniaceae. His next order, the Lamiales, includes several of the families with which we are concerned here. In the eleventh edition of the Engler *Syllabus* (by Engler & Diels) we find a very large order Tubiflorae, with Borraginaceae [*sic*], Verbenaceae, Labiatae, Scrophulariaceae, Myoporaceae, Bignoniaceae, and 16 other families. Gunderson (l.c.) in his two orders Polemoniales and Boraginales includes many of these families. It is clear, then, that the Bignoniaceae, in the opinion of many taxonomists, should be associated with the families of my negative series.

Chemically the family fits well into my series. Fifteen species belonging to 12 genera are negative to the HCl/methanol reagent ; eight species belonging to as many genera are negative to the test for leuco-anthocyanins, while two have given ' doubtful ' reactions. Raphides are absent from all species so far examined. HCN is apparently rare, for it has been reported in but one case.

Syringin is probably absent. I have obtained negative results from 14 species belonging to 12 genera, and two 'doubtful' cases.

(h) *Labiatae.*—As treated by Briquet (1895 or 1897) in the first edition of *Die natürlichen Pflanzenfamilien*, this is a large family. It might be considered to have 200 genera and more than 3200 species, most of them herbaceous. Junell (1934), in an extensive paper on the gynaecium and systematics of the Verbenaceae and Labiatae, suggests that many of the former family should be transferred to the latter :—

> 'Nach den Ergebnissen meiner Untersuchungen hat somit Verbenaceae nur die Tribus Verbenoideae zu umfassen. Labiatae hat die übrigen Tribus (ausschliesslich Stilboideae, vgl. S. 56) zu umfassen, die früher zu Verbenaceae gezählt wurden, sowie die Tribus, welche schon früher zu Labiatae gehorten . . .'

This would make the Labiatae an even larger family. It also points towards the probable lack of any real distinction between the two families. The Labiatae, then, 'should' resemble chemically the Verbenaceae and the other members of my negative series.

I have tested so far only a small fraction of the group, with the following results. All of the woody species subjected to the HCl/methanol reagent have given negative reactions. Leuco-anthocyanins seem to be absent. I have recorded several doubtful results here, and, in one case, a weakly positive reaction was indicated, but this was almost certainly due to anthocyanin present in the leaves before the test was made. Raphides have never been observed in the Labiatae, nor, to my knowledge, has HCN been recorded. Syringin may be present in some members of the family though this requires confirmation. It seems from this relatively small sampling that my negative series may be extended to include the Labiatae.

(i) *Scrophulariaceae.*—This is a family of much the same size as the Labiatae, having about 210 genera and nearly 3000 species. Most of the plants included here are herbaceous but some are woody. Almost all systematists place it in the Tubiflorae (or its equivalent). Bessey (l.c.) has an order Scrophulariales which includes Scrophulariaceae, Bignoniaceae and eight other families. Van Tieghem & Constantin (1918) have a similar order but include also the Labiatae, Myoporaceae and Verbenaceae. Cronquist (l.c.) also has an order of this name and puts the Scrophulariaceae as its first family. He says :—

> 'The other families of the Scrophulariales are derived directly or indirectly from the Scrophulariaceae.'

He does not include the Labiatae in this order but he does have (among others) the Bignoniaceae, which I have discussed above, and the Myoporaceae (see below).

I should, then, expect this family to fit into my negative series. To date I have examined only a small fraction of its members with the following results.

Eleven species, belonging to six genera, are all negative to the HCl/methanol reagent ; 12 species from 11 genera seem to lack leuco-anthocyanins, five others being classed as doubtful but probably negative. Raphides have not been seen in the family, and only one species—'*Linaria striata*'—is said to have a cyanogenetic glycoside. This should be most carefully checked, for 17 other species, belonging to 11 genera, have failed to yield HCN. Syringin appears to be absent from several species, but may be present in three of the dozen or so tested. These results are consistent, at least, with the view that the family belongs to my negative series.

(j) *Myoporaceae.*—We have seen above that this smallish family (five genera with about 110 species) is often classed with the Scrophulariaceae and 'related' families. Lindley (l.c.), more than a century ago, said that the Myoporaceae and the Verbenaceae might be united. If these views are correct then it should 'fit' into my negative series. Unfortunately I have but meagre information as to the chemistry of the Myoporaceae. One member, *Myoporum laetum* Forst. f. is negative to the HCl/methanol reagent. It and *M. acuminatum* R. Br. seem to lack leuco-anthocyanins, while *Oftia africana* Bocq. ex Baill. gives an obscure reaction (say Bate-Smith & Lerner, l.c.). Raphides appear to be absent from the group, but a positive reaction for HCN is given by two or more species, though absent from others. Petri (1912 or 1913) says *Eremophila maculata* F. Muell. yields HCN, a finding which Finnemore & Cox confirm, reporting the leaves to have the cyanogenetic glycoside prunasin. I have twice obtained a positive test for HCN with *Myoporum laetum*. This last species seems also to have syringin. This is, of course, too small a sampling to enable me to reach any definite conclusion as to the correct placing of the Myoporaceae. It will be of great interest to study other members of the family.

(k) *Rubiaceae*.—This very large family, which may have nearly 400 genera and close to 6000 species, is almost always made the type family of an order Rubiales. Its associates, according to many authors, are the Caprifoliaceae, Valerianaceae and Dipsacaceae. There is no general agreement as to the origin of the order. Rendle (l.c.), Wernham (1911–12), Gundersen (l.c.), and Pulle (1952) all consider it to be derived from or near to the Umbelliflorae. Hutchinson (1948, l.c.) relates the Rubiales to his Loganiales and Verbenales. If he is right then the Rubiaceae should fit into my negative series.

Here, for the first time in our discussion, we come to a family which is definitely heterogeneous by the standards employed so far. Let us consider the HCl/methanol test first. I have applied it to 27 species and have obtained positive results in five, weak or doubtful reactions in seven, and negative results in 15. The test for leuco-anthocyanins gives equally mixed results—positive in eight, doubtful in four, and negative in seven. Raphides are widely spread in the family. They are present in at least 159 species belonging to well over 100 genera. On the other hand they are lacking in more than 50 genera. Bremecamp has summarized his views as to relationships within the Rubiaceae in a recent paper (1954). He uses the presence or absence of raphides as an important character :—

> 'On arrive à des groupes plus naturels quand on classe les genres en vertu de caractères comme la structure du testa, le degré de développement de l'albumen, le type floral et la présence ou l'absence de raphides.'

He makes six subfamilies of which the last—Rubioideae—contains all the raphide-producing members of the family, and he places *Gaertnera*, *Hymenocnemis* and *Pagamea* here, rather than in the Loganiaceae, because they have raphides.

Cyanogenetic glycosides seem to occur in several members of the family, though apparently absent from others. Petrie (l.c.) reports HCN from *Pomax umbellata* Soland. ex Gaertn., there are old records of it from *Psydrax dicoccus* Gaertn., and it has been obtained from '*Canthium odoratum* Seem' and *C. vaccinifolium* F. Muell.

Syringin seems to be absent from many. I have recorded negative tests for 26 species belonging to 21 genera, and doubtful results from five.

I must conclude that this great family is, chemically speaking, a very mixed one. It is possible that further work will show that it should be divided. For the present I should, perhaps, exclude it from my negative series,

(l) *Caprifoliaceae*.—This family, which contains about 18 genera and 400 species, is nearly always associated with the Rubiaceae. Hutchinson (1948, l.c.) feels that it is not a natural family :—

> 'Although for the present we include *Sambucus* (the Elder), and *Viburnum*, with *Lonicera* and *Linnaea* in the Caprifoliaceae, I suspect this family to be of mixed origin. *Lonicera* and *Linnaea* are no doubt related, but the other two genera [H. is writing only about British plants] seem very different from them . . . *Viburnum* is no doubt related to *Sambucus* . . .'

This is not a new idea. *Sambucus*, at least, has long been thought to be out of line in the Caprifoliaceae, Höck (1892) proposing a separate family, Sambucacceae, for it.

Chemically speaking this family, like the Rubiaceae, is mixed. *Viburnum* and *Sambucus* often give positive HCl/methanol tests, though a few are doubtful, and one or two negative. Other members of the family are consistently negative to this test. Positive leuco-anthocyanin tests have been observed in ten species belonging to six genera, a doubtful test in one, and negative tests in 14 species belonging to six genera. Further tests are obviously desirable. Raphides are constantly absent. The test for cyanogenetic glycosides yields mixed results. *Sambucus* is known to have these substances. Some species of *Viburnum* also give positive tests but they are not quite typical, and the presence of HCN should be confirmed by other methods. Most of the other members of the family seem not to have cyanogenetic glycosides. Syringin apparently is absent from more than 60 of the species tested ; it may be present in a very few.

On nearly every count, then, the reactions of the family are mixed and I must consider it, like the Rubiaceae, to require further investigation. In an earlier paper (Gibbs, l.c., p. 26) I expressed the opinion that the Caprifoliaceae (if *Viburnum* and *Sambucus* be removed) might end my negative series. I am now less certain of this. The results, however, are not inconsistent with the view that the Rubiaceae and the Caprifoliaceae are related to each other.

TABLE I.—A series of families negative to the HCl/methanol reagent

Fractions indicate numbers of genera and species thus 2/3 means 3 spp. belonging to 2 genera.

Families	HCl/methanol			'Leuco-anthocyanins'			Raphides		HCN		'Syringin'		
	+	?	−	+	?	−	+	−	+	−	+	?	
Aquifoliaceae (4/416)	...	1/1	2/23	1/2	1/1	1/2	...	4/10	...	2/5	...	...	2/11
Salvadoraceae (4/9) . .	...	...	2/2	...	...	...	...	4/5	...	...	...	...	2/2
Oleaceae (22/500)	...	...	15/99	...	...	7/14	?	7/14	...	10/21	15/42	5/12	6/12
Loganiaceae (32/800) .	...	...	7/18	...	...	5/5	...	27/59	...	7/12	1/1	2/5	7/7
'Woody Boraginaceae' (13/300)	...	...	4/8	...	1/1	1/2	...	8/16	...	3/4	2/2	...	3/5
Verbenaceae (100/2600)	...	...	22/48	...	3/3	11/16	...	52/78	1/1?	18/37	3/3	9/13	18/41
Bignoniaceae (110/750)	...	...	12/15	...	2/2	8/8	...	71/72	1/1	13/15	...	2/2	12/14
Labiatae (200/3200)	...	...	9/10	1/1[1]	9/9	21/28	...	82/84	...	19/23	2/2	4/4	3/3
Scrophulariaceae . . . . (210/3000)	...	...	6/11	...	4/5	11/12	...	72/78	1/1	11/17	...	3/3	5/10
Myoporaceae (5/110)	...	...	1/1	...	1/1	1/2	...	5/5	2/2	2/3	1/1	...	...
Rubiaceae (400/6000)	4/5	6/7	13/15	7/8	3/4	7/7	112/159	52/57	3/4	12/15	...	5/5	21/26
Caprifoliaceae (18/400)	2/30	2/3	9/51	6/10	1/1	6/14	...	12/40	2/4[2]	8/59	...	5/12	7/57

Probably due to anthocyanin in leaves before test.
Two of these doubtful.

B. *A HCl/Methanol Positive Series*

As I noted on p. 216, Gundersen (l.c.) considers that the Theaceae, Ericaceae, and Cyrillaceae should be studied from all points of view. With this in mind I started to examine such members of these three families as I could obtain and found them to be strongly positive to the HCl/methanol reagent. This led me to extend my studies to ' related ' families and it soon became clear that a positive series can be constructed. The member-families of this series may now be briefly considered.

(a) *Dilleniaceae.*—It is probable that this family, which contains perhaps 11 genera and 275 species, is very near the starting point of our positive series. I discussed its taxonomy fairly fully in an earlier paper (Gibbs, l.c., pp. 26–28) so may omit it on this occasion. Seven species, belonging to the genera *Candollea*, *Dillenia*, *Hibbertia*, and *Wormia*, have been available to me and all have given positive reactions with the HCl/methanol reagent. Bate-Smith & Lerner (l.c.) found *Candollea tetrandra* Lindl. to give a positive test for leuco-anthocyanins, while I have found *Hibbertia dentata* R. Br. and *H. volubilis* Andr. to react similarly. Raphides are present in most, if not in all members. They have been recorded in more than 30 species belonging to eight genera, but are said to be small and unorientated in some cases. HCN has not been recorded, although tests for it have been made on 11 species belonging to three genera. Syringin is probably absent : I have recorded one doubtful case.

If these characters are to be considered typical of my positive series then we shall expect related families to be positive to the HCl/methanol reagent and to the test for leuco-anthocyanins, to possess raphides, to lack HCN, and to lack syringin.

(b) *Actinidiaceae.*—This little family may be considered to contain three or four genera and about 270 spp. *Actinidia* itself has been put in the Camelliaceae (Theaceae) and in the Clethraceae ; *Clematoclethra* has been included in the Dilleniaceae or as an ' anomalous ' genus in the Theaceae ; *Saurauia* has been placed in Dilleniaceae, Clethraceae, and Saurauiaceae ; while *Sladenia* has sometimes been put into the Theaceae.

The chemistry of this group, then, should approach the Dilleniaceae on the one hand, and the Theaceae on the other. Using the HCl/methanol reagent I have obtained positive reactions with five species belonging to three of the genera. Bate-Smith & Lerner (l.c.) found *Actinidia chinensis* Planch. to have leuco-anthocyanins and I have obtained a positive result with *A. arguta* Miq. Raphides are present in all but *Sladenia*, and it has been suggested that this genus would indeed be better placed in the Theaceae, a family typically devoid of raphides, as we shall see. I have no record of HCN in the family. Syringin probably is absent. These results, incomplete as they are, suggest that the Actinidiaceae are properly placed here.

(c) *Bixaceae.*—I shall consider this family to consist only of the genus *Bixa* with one or two species. It has been variously placed. In the Engler & Diels's scheme (l.c.) it is in the Parietales and therefore an associate of Dilleniaceae, Actinidiaceae, Theaceae, etc. *Bixa orellana* L. is positive to the HCL/methanol test, has leuco-anthocyanins, lacks HCN, and seems not to have syringin. Raphides are absent—this is true also of the Theaceae (as restricted, see below) and in the later families of my positive series. These facts are consistent with the placing of Bixaceae here.

(d) *Theaceae* (*Ternstroemiaceae*, *Camelliaceae*.)—This moderate-sized family is considered here to have 27–30 genera and about 500 species. Many taxonomists bring it into close association with Dilleniaceae, Actinidiaceae, etc., as we have seen. It should, therefore, be positive to the HCl/methanol reagent, have leuco-anthocyanins, perhaps have raphides, lack HCN, and lack syringin. At least 14 species belonging to seven genera have been found to be strongly positive with HCl/methanol. Three species have leuco-anthocyanins, one may have them. Bate-Smith & Lerner (l.c.) report a positive reaction for these substances in *Camellia sinensis* (L.) O. Ktze., but I have twice got a negative reaction![1] According to Hess (1936) raphides are absent from almost all members of the family. He found them only in *Tetramerista*, which he considers to be misplaced, but they have been found also in *Pelliciera* and in *Trematanthera*. There are, perhaps, good reasons for excluding these three genera from the family which then is completely without raphides. I know nothing further about the chemistry of these three genera. It is interesting to note than Hallier (1912) placed *Pelliciera* and *Tetramerista* doubtfully in the Marcgraviaceae—a family which has raphides, while he included *Trematanthera* in *Saurauia*—which also has raphides. Cyanogenetic glycosides have not, I think, been found in the Theaceae: I have negative results from four species. Syringin is probably absent. It would seem, then, that the family fits well into my positive series.

(e) *Clethraceae.*—The old idea that the sympetalous dicotyledons form a natural group is, of course, now considered to be doubtful. The modern view is that there has been a repeated 'tendency' toward sympetaly and that sympetalous families represent a number of ends of evolutionary lines. The difficulty, however, is to decide how many ends there are, and of what lines they are the ends! The families grouped as the Bicornes or Ericales are essentially sympetalous, but may well have their origin in families such as I have been considering above. Thus Hutchinson (1948, l.c.) says:—

> 'The origin of the family Ericaceae is probably to be found in the tea family, Theaceae, which shows relationship with *Rhododendron* through the Saurauiaceae [included by us in Actinidiaceae], a small family close to the Theaceae. The exotic Clethraceae [H. is writing about British plants], whilst no doubt closely allied to Ericaceae, are also very near Theaceae, their petals being free.'

If Hutchinson is right then the chemistry of the Clethraceae should be the chemistry of my positive series. The family is a small one, with but two genera and 31 species. Five species of *Clethra* have been found to be positive to the HCl/methanol reagent, while four have leuco-anthocyanins. Raphides seem to be absent from *Clethra* and also from the other genus—*Schizocardia*. HCN may be given by the seeds of *Clethra*—but my results need to be checked. I have not detected HCN in the leaves of *C. arborea* Ait. Syringin appears to be absent.

Apart from the possible occurrence of HCN these results seem to be consistent with the view that the family is near to the Theaceae.

(f) *Ericaceae.*—I shall consider this family to include the subfamilies Rhododendroideae, Arbutoideae, Ericoideae, and Vaccinioideae, but to exclude the Pyroloideae and Monotropoideae. I then have a group of about 70 genera and 1900 species. Of these I have tested 83 species belonging to 30 genera with the HCl/methanol reagent and have obtained a positive reaction in every case. Results are equally clear-cut with the test for leuco-anthocyanins, eight species belonging to seven genera giving a positive reaction. The family is also homogeneous with respect to raphides—none have been observed. I obtained many negative results when testing for cyanogenetic glycosides and had become almost convinced that the Ericaceae are completely devoid of these compounds. However, an old record by Mirande (1913) of HCN from *Erica multiflora* L. led me to look further. A friend on the West coast, and an assistant, subsequently obtained positive tests in the case of *E. vagans* L.

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[1] In the discussion Dr Bate-Smith said that leuco-anthocyanins were easily detected in some varieties of tea, but not in others. This was confirmed by Dr Roberts. Roberts *et al.* (J. Sci. Food Agric. 1956, **7**, 253) have identified leuco-delphinid as the predominant leuco-anthocyanin in two samples of unprocessed tea-leaf.

and I have recently confirmed their findings. Seeds of many species have been tested, as well as leaves. So far as we know HCN has been found in this family only in the two species of *Erica* mentioned above unless a very doubtful record from the seeds of a *Vaccinium* be accepted. This rare occurrence indicates how necessary it is to make as complete a survey as possible for every chemical character before drawing any general conclusions.

Syringin appears to be absent from the group—I have recorded negative results from 79 species belonging to 33 genera, two doubtful cases, and no certainly positive ones. The Ericaceae, then, may be taken as typical of my positive series.

(g) *Pyrolaceae* (*Pirolaceae*).—Some authors have included this small group of plants (about 10 genera with 32 species) in the Ericaceae. They are more or less herbaceous and so do not lend themselves to the HCl/methanol test. As noted above, however, the development of a red colour with the reagent for syringin (1 : 1 H_2SO_4) is almost invariably correlated with a positive reaction with HCl/methanol. *Chimaphila umbellata* Nutt., *Pyrola rotundifolia* L. var. *americana*, and *P. secunda* L. have all given a red colour with 1 : 1 H_2SO_4. *Chimaphila umbellata* has given a doubtfully positive and *Pyrola elliptica* Nutt. (identification uncertain) a strongly positive test for leuco-anthocyanins. Raphides and syringin seem to be absent.

These results are much as those from the Ericaceae and are consistent with a close relationship between the two groups.

(h) *Epacridaceae*.—So similar to the Ericaceae are the members of this moderate-sized family (25–30 genera and 350 species) of the southern hemisphere that they have been called ' the Ericaceae of Australia '. I should expect the two families to be very similar chemically and my tests seem to bear this out. Six species, belonging to four genera have all been found to give strongly positive reactions to the HCl/methanol reagent. *Epacris longiflora* Cav. gives a positive reaction for leuco-anthocyanins. Raphides are absent from the family. Cyanogenetic glycosides may be absent. I have records of negative tests on 22 species belonging to ten genera, but one doubtfully positive test on *Brachyloma daphnoides* Benth. is reported. This should be checked with care. Syringin has been tested for in five species, belonging to four genera, with negative results. The Epacridaceae do then, resemble the Ericaceae in their chemistry.

(i) *Diapensiaceae*.—This is a small family (six genera and about 12 species) which has been included in the Ericales by such taxonomists as Bessey (l.c.), Rendle (l.c.) andGundersen (l.c.). In the Engler & Diels system (l.c.) it has been made a separate order Diapensiales and placed immediately before the Ericales.

Unfortunately I have had little access so far to the members of the family. Leaves of *Galax aphylla* L. have given a negative test for leuco-anthocyanins, which is out of line with a position here. Raphides appear to be absent from all genera. HCN, from my tests, is probably lacking from *Galax*, and I have found no reference to its occurrence in the Diapensiaceae.

(j) *Empetraceae*.—This is one of our most interesting families, taxonomically speaking, for there has been great discussion as to its position. Bessey (l.c.) placed it in the Sapindales next to Coriariaceae. Van Tieghem & Constantin (l.c.) have it in the Pittosporales. Rendle (l.c.) puts it doubtfully in the Celastrales. Hallier, as long ago as 1912, considered the group to be either a tribe of the Ericaceae, or to be descended from it, a view shared by Samuelsson (1913) who put it in the Bicornes (Ericales) with Ericaceae, Clethraceae, Epacridaceae, Pyrolaceae and Diapensiaceae. The modern tendency is to follow this placing, and we find Wettstein (1935), Gundersen (l.c.), Pulle (l.c.), Cronquist (l.c.) and others including the Empetraceae in an order Bicornes or Ericales. If this modern view is correct then the Empetraceae should be positive to the HCl methanol and leuco-anthocyanin tests, should lack raphides and probably lack HCN, and should not have syringin. Through the kindness of friends I have had access to all three genera of the family. *Ceratiola ericoides* Michx., *Corema conradi* Torr., *Empetrum hermaphroditum* (Lange) Hagerup and *E. nigrum* L. all give very strong HCl/methanol tests. *Empetrum hermaphroditum* has leuco-anthocyanins. All lack raphides and all seem to lack HCN. Syringin is probably absent, though I recorded *E. nigrum* as doubtfully negative to my test. These results are certainly consistent with the view that the family belongs in my positive series.

(k) *Cyrillaceae.*—This is another smallish family of uncertain affinities. Bentham & Hooker (1862–83) have it as Ordo XLVIa after Ilicineae (Aquifoliaceae) in their Olacales. Bessey, Hutchinson, and Pulle have all placed it in the Celastrales. Others have put it in the Sapindales, and yet others in the vicinity of the Ericales. Gundersen (l.c.), though including it in the Celastrales, remarks that the 'characters of *Cyrilla* suggest Ericaceae'. I have noted above that he suggests that the three families Theaceae, Ericaceae, and Cyrillaceae should be investigated as a group.

Unfortunately members of the Cyrillaceae have not been readily accessible to me. What evidence I have, however, is consistent with the view that this family belongs to my positive series. *Cyrilla racemiflora* L. gives a positive HCl/methanol test and seems to lack syringin. It and *Cliftonia*, at least, probably lack raphides. I have found no reference to HCN in the family. For the moment, then, the Cyrillaceae may be considered to end my positive series.

TABLE II.—A series of families positive to the HCl/methanol reagent

	HCl/methanol			'Leuco-anthocyanins'			Raphides		HCN		'Syringin'		
Families	+	?	−	+	?	−	+	−	+	−	+	?	−
illeniaceae (11/275)	4/7	...	...	2/3	...	...	8/31[1]	...	...	3/11	...	1/1	4/6
ctinidiaceae (4/285)	3/5	...	...	1/2	...	...	3/52	1/1[2]	...	1/1	...	1/2	3/3
ixaceae (1/1 or 2)	1/1	...	...	1/1	...	...	...	1/1	...	1/1	...	...	1/1
heaceae (27–30/500)	7/14	...	...	2/3	1/1	1/1[3]	3/5[4]	17/23	...	4/4	...	1/1	6/12
lethraceae (2/31)	1/5	...	...	1/4	...	...	...	2/6	1/2?	1/1	...	...	1/4
ricaceae (70/1900)	30/83	...	...	7/8	...	...	...	46/99	2/3[5]	24/138	...	2/2	33/79
yrolaceae (10/32)	...	...	...	1/1	1/1	...	...	4/5	...	...	...	...	2/3
pacridaceae (25–30/350)	4/6	...	...	1/1	...	...	...	28/29	1/1?	10/22	...	...	4/5
iapensiaceae (6/12)	...	...	...	...	...	1/1	...	6/6	...	1/1	...	...	...
mpetraceae (3/6)	3/4	...	...	1/1	...	...	...	3/4	...	3/4	...	1/1	3/3
yrillaceae (4/20 ?)	1/1	...	...	...	...	...	...	2/2	...	...	...	...	1/1

4/7 they are small and unarranged.
adenia, which should, perhaps, be in the Theaceae.
negative reaction in *Thea sinensis*. Bate-Smith & Lerner report a positive reaction.
tramerista, *Pelliciera*, and *Trematanthera*. These should, perhaps, be excluded from the Theaceae.
e result doubtful.

DISCUSSION

It will be obvious to the reader of the above pages that I have only scratched the surface of the subject of biochemistry as an aid to solving taxonomic problems. Before I can draw safe conclusions from my results I must establish the 'chemical characters' of the taxa—be they varieties, species, genera, families, or orders. It will be a long time before I can do this for any major group.

It does seem that certain families (and perhaps others) are constantly negative to the HCl/methanol test, while others are as constantly positive. These characters go rather closely with the absence and presence respectively of leuco-anthocyanins as indicated by the test described. So much did this appear to be the case that I began to wonder if reactions to the two tests are due to the same substance or substances. There are exceptions, however, and this is brought out particularly in the Caprifoliaceae, which has given such mixed results in general. Table III summarizes observations for this family with respect to these two tests.

TABLE III.—Caprifoliaceae. Summary of results of HCl/methanol and leuco-anthocyanin tests

Genera	HCl/methanol			Leuco-anthocyanin		
	+	?	—	+	?	—
Abelia (25)	...	...	3	1	...	...
Diervilla (10)	...	...	4	2	...	...
Kolkwitzia (1)	...	...	1	1	...	...
Leycesteria (3)	...	1	...	...	...	1
Linnaea (1 ?)	...	...	...	...	1	...
Lonicera (100)	...	...	28	...	...	8
Symphoricarpos (15)	...	...	5	...	...	1
Triosteum (8)	...	...	3	...	...	1
Weigela (12)	...	...	5	1	...	...
Sambucus (20)	5	2	1	1	...	2
Viburnum (120)	25	...	1	4	1	1
Family (18/400)	2/30	2/3	9/51	6/10	1/1	6/14

It should be emphasized that the tests have not always been applied to the same species. For example in the case of *Diervilla* I note that *D. japonica* DC., *D. rivularis* Gatt, *D. sessilifolia* Buckl. and *D. splendens* Kirchn. give negative tests with the HCl/methanol reagent, while *D. floribunda* Sieb. & Zucc. and ‘ *D. venosa* (*D. venusta*?) ’ according to Bate-Smith & Lerner (l.c.) give positive reactions with the test for leuco-anthocyanins.

In the Rubiaceae there is, in the few cases where I have tested the same plants with both reagents, a fairly close correlation (Table IV).

TABLE IV.—Rubiaceae. Results of HCl methanol and leuco-anthocyanin tests

Plants tested	HCl/methanol			Leuco-anthocyanin		
	+	?	—	+	?	—
Brachytome wallichii	...	...	1	...	...	1
Coffea sp.	...	...	1	...	1	...
Gardenia jasminoides	...	...	1	...	...	1
Cephalanthus occidentalis	1	...	...	1	...	...
Ixora coccinea	1	...	...	1	...	...
Psychotria carthaginensis	1	...	...	...	1	...
Rondeletia odorata	...	1	...	1	...	...
All tested	4/5	6/7	13/15	7/8	3/4	7/7

The use of the test for leuco-anthocyanins is fairly new, and many more plants must be examined before I dare to generalize.

The present communication amplifies in several respects a previous paper (Gibbs. l.c.). It adds a few families to my negative series and shows that the test for leuco-anthocyanins supports my previous conclusions.

One is tempted to speculate as to the evolutionary nature of some of the chemical characters dealt with above. It seems obvious that the split into HCl/methanol-positive and HCl methanol-negative lines came early in the evolution of the series discussed. The same is probably true for presence and absence of leuco-anthocyanins. Raphides seem never to occur in my HCl methanol-negative series. They *do* occur in one group of the Rubiaceae, but that may be of independent (and recent) origin. In the HCl methanol-positive series, on the other hand, raphides may be considered to be primitive—occurring in Dilleniaceae, Actinidiaceae and the three genera *Pelliciera*, *Trematanthera*, and *Tetramerista* (which may belong elsewhere), and not in any of the more advanced families of the series.

The occurrence of HCN might be considered to be an advanced character, but it is so rare in both series as to be of little value in my arguments.

The ability to produce syringin (or something giving a bluish colour with 1 : 1 H_2SO_4) seems to be restricted to my HCl/methanol-negative series. Until actual isolation of syringin is carried out we must be cautious, however, in attributing the blue colour with sulphuric acid to this glycoside.

I am indebted to so many friends for assistance that it would be invidious to single out individuals for thanks. I am grateful to all who have helped by sending me plant material, by providing research facilities at their institutions, or by making tests. The National Research Council of Canada has provided funds for much of this work : support which is gratefully acknowledged.

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THE DISTRIBUTION AND BIOGENESIS OF THE CUCURBITACINS IN RELATION TO THE TAXONOMY OF THE CUCURBITACEAE

By P. R. ENSLIN & S. REHM

INTRODUCTION

THE presence in various Cucurbitaceae of purgative bitter principles has been known since ancient times. Pharmaceutical preparations which are still used in modern medical practice include colocynth from *Citrullus colocynthis*, bryonia from species of *Bryonia* and elaterium from *Ecballium elaterium.* Bitterness occurs sporadically in cultivated cucurbits, presenting a real danger to human health (1). Interest in these substances was recently revived by the discovery at the National Cancer Institute in Bethesda that some possess anti-tumour activity (2).

These bitter principles occur very widely distributed in the Cucurbitaceae. Of the 850 species and 90-100 genera, bitterness has been reported in 88 species. A systematic search for bitter principles revealed that the greater majority of species investigated contain these substances in some part or other of the plant at some stage or other of its development.

Most of the substances described in the older literature are badly characterized and may be mixtures of many compounds. Only relatively few well-defined substances have been isolated, the best known example being α-elaterin from *Ecballium elaterium* and *Citrullus colocynthis.* Certain species contain pentacyclic triterpenoid saponins (e.g., *Echinocystis fabacea* Naud., *Momordica cochinchinensis* Spreng. and *Luffa operculata* Cogn.).[1]

Recently we succeeded in isolating ten crystalline bitter substances, provisionally named the cucurbitacins, from various species. These substances appear to be related to the tetracyclic triterpenes (3, 4).

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[1] See literature cited in ref. (4).

Chemistry

Most bitter principles occur in nature as glycosides in complicated mixtures. Cucurbitacins A, C and F, however, occur without the sugar moiety. All attempts to separate and crystallize the glycosides have failed so far. Fortunately many species contain a very active glucosidase, named elaterase by Berg (5), which hydrolyses the glycosides to the free aglycones. These can then be separated and purified on cellulose powder columns previously impregnated with formamide (4). Elaterase has been obtained (6, 7) in a relatively pure state showing only a single $S_{4.2}$ component in the ultra-centrifuge, but still showing two components when examined by electrophoresis. Under optimum conditions of temperature and pH (37° C. and pH 5·2) 100 mg. of elaterin mono-glucoside is completely hydrolysed within 1 hr. with 0·05 mg. of purified elaterase. This enzyme is also capable of splitting off glucose from a variety of other glycosides notably steroidal saponins (8), the diterpene β-D-glucoside, darutoside (9), the cardiac glycosides scilliroside, digilanide A and k-strophantin-β (10).

The molecular formula of elaterin and the other cucurbitacins remained uncertain for many years, until Rivett & Herbstein (11) reported accurate X-ray determinations, which showed that the acetoxy-containing cucurbitacins A, B, C and E (α-elaterin) possessed the formulae $C_{32}H_{46}O_9$, $C_{32}H_{48}O_8$, $C_{32}H_{50}O_8$ and $C_{32}H_{44}O_8$ respectively. The $C_{32}H_{44}O_8$ formula for elaterin was elegantly proved in the following way: Lavie (12) postulated that ecballic acid, first prepared by Borsche & Diacont (13), is formed according to the reaction $C_{28}H_{38}O_7 + 2H_2O \rightarrow C_{26}H_{38}O_7 + CH_3COOH$. An α-diketo grouping undergoes a benzilic acid rearrangement to give an α-hydroxy acid. Rivett & Herbstein (11), however, demonstrated that acetoin $CH_3.CHOH.CO.CH_3$ is also produced in good yield during the reaction as the result of a retro-aldolization, thus giving an overall reaction $C_{32}H_{44}O_8 + 3H_2O \rightarrow C_{26}H_{38}O_7 + C_4H_8O_2 + C_2H_4O_2$. An equivalent weight determination on ecballic acid left no doubt as to its molecular formula.

The molecular formulae and properties of all the known crystalline cucurbitacins are tabulated in Table I.

Table I

Crystalline cucurbitacins	Tentative formulae	m.p.	[α]D.
A	$C_{32}H_{46}O_9$	207–208°	+97° (EtOH)
B	$C_{32}H_{48}O_8$	184–186°	+88° (EtOH)
C	$C_{32}H_{50}O_8$	207–207·5°	+95° (EtOH)
D	$C_{30}H_{46}O_7 \cdot \frac{1}{2}H_2O$	151–152°	+52° (EtOH)
E	$C_{32}H_{44}O_8$	234·5°	−62° (Chlf.)
F	$C_{30}H_{48}O_7$	244–246°	+38° (EtOH)
G	$C_{30}H_{52}O_9$	149–150°	...
I	$C_{30}H_{44}O_8$	148–148·5°	...
J	$C_{30}H_{44}O_8$	196–198°	...
K	...	137–141°	...
L	$C_{30}H_{46}O_7 \cdot \frac{1}{2}H_2O$	122–127°	−41° (EtOH)

All bitter principles contain two or more alcoholic hydroxyl groups and cucurbitacins A, B, C and E also contain one acetoxy group. The presence of several keto groups is a very characteristic structural feature of these substances. In cucurbitacins A, B, C, D, E, F and I one of the keto groups is α, β-unsaturated. Cucurbitacins B, D, E, G, I, J, K and L contain a diosphenol (α-diketone) grouping which can combine with glucose to form naturally occurring enolglycosides (3, 4).

TABLE II

Species[1]	Origin	Part of plant[2]	Cucurbitacins											
			A	B	C	D	E	F	G	H	I	J	K	L
Acanthosicyos horrida Welw.	Nambi, SW. Afr.	f[3]	...	++	...	++	...	...	tr	tr	...	...	...	...
		r[4]	...	(+++)	...	(+++)	...	...	(++)	(++)	...	...	...	...
Bryonia alba Linn.	Culta	r	...	+	...	tr	+	...	...	...	tr	...	...	...
Bryonia dioica Jacq.	Culta	r	...	+	...	tr	+	...	...	...	tr	...	...	...
Citrullus colocynthis (L.) Schrad.	Algeria, Egypt, Israel, Sudan	f	...	...	...	...	(+++)	...	...	...	...	...	...	...
		l	...	(+)	...	...	(+)	...	...	...	...	...	...	...
Citrullus ecirrhosus Cogn.	Namib, SW. Afr.	f	...	...	...	...	(+++)	...	...	...	...	...	...	...
		l	...	...	...	...	(+)	...	...	...	...	...	...	...
		r[4]	...	...	...	...	(+++)	...	...	...	(+++)	(+++)	(+++)	(+++)
Citrullus naudinianus (Sond.) Hook. f.	N. Tvl., SW. Afr.	f	...	+	...	+	...	...	tr	tr	...	...	...	...
		r	...	(+++)	...	(+++)	(+++)	...	(++)	(++)	(+++)	(++)	(++)	...
Citrullus vulgaris Schrad.	Cape Prov., SW. Afr.	f	...	...	...	...	(++)	...	...	...	...	...	...	...
		l	...	...	...	...	+	...	...	...	tr	...	...	...
Coccinia adoensis (A. Rich.) Cogn.	Tvl.	f[3]	...	+	...	tr	...	...	...	...	...	...	...	...
Coccinia hirtella Cogn.	Natal	f	...	(+)	...	...	...	...	...	...	...	...	...	...
Coccinia quinqueloba (Thunb.) Cogn.	Cape Prov.	f	...	(+)	...	...	...	...	...	...	...	...	...	...
Corallocarpus sphaerocarpus Cogn.	SW. Afr., N. Rhod.	r	...	++	...	+	...	...	tr	tr	...	...	...	...
Cucumis africanus Linn. f.	Tvl., Swaziland	f	...	++	...	tr	...	...	...	...	...	...	...	...
Cucumis angolensis Hook. f. (= *Cucumis dinteri* Cogn.)[5]	SW. Afr.	f	...	+	...	+++	...	tr	+		...	...	...	...
		l	...	+	...	++	...	++	...	...	...	...	...	...
		r	...	+	...	++	...	+	+		...	...	...	...
Cucumis dipsaceus Ehrenb.	Culta	f	...	++	...	+	...	...	...	...	...	...	...	...
Cucumis heptadactylus Naud.	N. Tvl., Cape Prov.	f	...	++	...	+	...	...	...	...	...	...	...	...
		r	...	++	...	++	...	...	++	++	...	...	...	...
Cucumis hirsutus Sond.	Tvl.	r	...	+	...	++	...	...	++	++	...	...	...	...
Cucumis hookeri Naud.	N. Tvl., SW. Afr.	f	++	++	...	++	...	...	tr	tr	...	...	...	...
Cucumis humifructus Stent	N. Tvl.	f	...	[illegible]	...	tr	...	...	...	...	...	...	...	...
Cucumis kalahariensis	SW. Afr.	f	...	+++	...	+	...	...	...	...	...	...	...	...
Cucumis leptodermis Schweick	O.F.S., Cape Prov.	f	+++	tr	...	tr	...	...	...	...	...	...	...	...
Cucumis longipes Hook. f. (= *Cucumis ficifolius* A. Rich.)[5]	SW. Afr., N. Tvl., S. Rhod.	f	...	+++	...	+	...	...	tr	tr	...	...	...	...
Cucumis metuliferus E. Mey. ex Naud.	N. Tvl., SW. Afr.	f	...	tr	...	...	...	...	...	...	...	...	...	...
Cucumis myriocarpus Naud.	Tvl., O.F.S., Australia	f	+++	+	...	+	...	...	...	...	...	...	...	...
Cucumis prophetarum Linn. f.	Israel, Sudan	f	...	++	...	+	...	...	tr	tr	...	...	...	...
Cucumis pustulatus Hook. f.	SW. Afr.	f	...	++	...	+	...	...	...	...	...	...	...	...
Cucumis sativus Linn. var. 'Hanzil'	Culta		...	...	+++	...	...	...	...	...	...	...	...	...
			...	...	+	...	...	...		...	...	...	...	...

Cucurbita foetidissima H. B. K.	Culta	l	...	(+)	...	...	(++)	...	...	...	...	...	...	...
		young r	...	(++)	...	...	(tr)	...	...	...	...	...	...	...
		old r	...	+++	...	++	tr	...	tr	tr	...	...	...	...
Cucurbita mixta Pangalo	Culta[6]	f	...	$(\underline{+})$	...	...	...	...	...	...	...	...	...	...
Cucurbita okeechobeensis	Culta	f	...	...	...	++	...	...	...	...	++	tr	tr	...
		l	...	...	...	+	...	...	...	...	+	tr	tr	...
		r	...	tr	...	+	...	...	...	...	+	...	...	...
Cucurbita pepo Linn. convar. *microcarpina* Greb. (=*Cucurbita texana* (Scheele) A. Gray)[5]	Culta[6]	f	...	...	...	...	$(\underline{+++})$	...	...	...	...	...	...	...
Cucurbita pepo Linn. var. *ovifera* (Linn.) Alef.	Culta	f	...	(++)	...	$(\underline{++})$	(+++)	...	(tr)	(tr)	(++)	(tr)	(tr)	...
Ecballium elaterium (L.) A. Rich.	N. Africa	f	...	(++)	...	(+)	$(\underline{++})$	...	...	...	(+)	...	...	...
		l	...	+	...	+	+	...	...	...	+	...	...	...
		r	...	+	...	$\underline{++}$	tr	...	+	+	+	...	...	...
Echinocystis lobata Torr. et Gray	Culta	f	...	++	...	...	+	...	...	...	...	...	...	...
		r	...	...	...	...	(+)	...	...	...	(tr)	...	...	...
Echinocystis wrightii Cogn.	Culta	f	...	(+)	...	...	(+)	...	...	...	...	...	...	...
Gerrardanthus spec.	E. Africa	r	...	tr	...	+	...	...	+	+	...	...	...	...
Kedrostis africana (L.) Cogn.	Tvl.	r	...	++	...	++	++	...	+	+	++	+	+	...
Kedrostis foetidissima (Jacq.) Cogn. var. *microcarpa* Cogn.	Tvl.	r	...	+	...	tr	+	...	...	...	+	...	...	...
Kedrostis nana (Lam.) Cogn.	Cape Prov.	r	...	++	...	+	+	...	tr	tr	...	...	...	...
Kedrostis spec. (*Toxanthera natalensis* Hook. f.)	Tvl., SW. Afr.	r	...	++	...	++	...	...	++	++	...	...	...	...
Lagenaria mascarena Naud. = *Sphaerosicyos sphaericus* (E. Mey. ex Sond.) Cogn.)[5]	S. Rhod.	f	...	+	...	+	tr	...	tr	tr	tr	...	...	...
	N. Tvl.	f	...	++	...	+	...	...	tr	tr	...	...	...	...
	N. Tvl.	r	...	++	...	tr	...	...	...	...	...	...	...	...
Lagenaria siceraria (Mol.) Standl.	Tvl.	f	...	$\underline{++}$	...	+	...	...	tr	tr	...	...	...	...
		l	...	+	...	...	...	...	...	...	...	...	...	...
		r	...	+	...	+	tr	...	...	...	...	...	...	...
Luffa acutangula (Linn.) Roxb.	Culta	r	...	++	...	tr	...	...	...	...	...	...	...	...
		s	...	+	...	tr	...	...	tr	tr	...	...	...	...
Melothria punctata (Thunb.) Cogn.	Cape Prov.	r	...	+	...	++	...	...	tr	tr	...	...	...	...
Peponium mackenii (Naud.) Engl.	Cape Prov.	f	...	...	...	...	(++)	...	...	...	...	...	...	...
		r	...	...	...	...	++	...	...	...	+	...	...	...
Sicyos angulata Linn.	Culta	s	...	+++	...	...	...	...	...	...	...	...	...	...
Telfairia pedata (Smith) Hook. f.	E. Africa	s[7]	...	++	...	++	+	...	tr	tr	...	...	...	...
Trochomeria debilis (Sond.) Cogn.	N. Tvl.	r	...	+	...	+	...	...	+	+	...	...	...	...
Trochomeria sagittata (Harv.) Cogn.	Cape Prov.	r	...	+	...	+	...	...	+	+	...	...	...	...

Distribution of the Cucurbitacins

+++ Amount of bitter principle 0·1 per cent or higher;
++ amount of bitter principle 0·01–0·09 per cent;
+ amount of bitter principle 0·001–0·009 per cent;
tr trace of bitter principle (less than 0·001 per cent)
() bitter principle present exclusively or mainly as glycoside;
—— Underlined symbols indicate that the bitter principle has been isolated in the crystalline state and chemically identified.

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[1] The names of the South African species are subject to revision. A taxonomic survey of the Cucurbitaceae of Southern Africa is at present being undertaken by Dr A. D. J. Meeuse, Nat. Herb., Pretoria.

[2] f = fruits, l = leaves, r = roots, s = seeds.

[3] Unripe fruits; ripe fruits are not bitter.

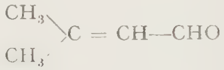
[4] Dry roots.

[5] The synonym quoted in brackets was used in our paper on elaterase (6).

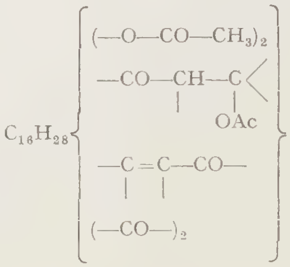
[6] The same strain was used by Grebenščikov for genetical studies.

[7] Dry fibrous cover surrounding seeds.

The isolation of 1,2,8-trimethylphenanthrene from the dehydrogenation of previously reduced cucurbitacin A indicated a possible structural relationship to the tetracyclic triterpenes (14). The formation of senecio aldehyde



on oxidation of cucurbitacins A and C with chromic acid, threw light on the nature of the side chains present. Mild chromic acid oxidation of the acetates of cucurbitacin A or dihydro cucurbitacin A gave, in good yield, a crystalline product which is being extensively studied. Various reactions performed on this product revealed the following partial structure (15) :—



Distribution of Bitter Principles in Mature Plants

For a systematic study of the distribution of the cucurbitacins in the various parts of a plant at different stages of development, a very effective paper chromatographic method was evolved (16, 17). Excellent separations are obtained on filter paper impregnated with formamide, using ethyl acetate-benzene and chloroform-benzene mixtures as mobile phases. Characteristic colour reactions with potassium permanganate-copper acetate, ferric chloride, tetrazolium salts, phosphomolybdic acid and vanillin in phosphoric acid enable one to distinguish any of the 11 crystalline cucurbitacins and the amorphous cucurbitacin H from one another.

In many cases the presence of certain cucurbitacins was also established by means of isolation and chemical characterization. In all cases the results confirmed those obtained by paper chromatography.

In addition to the species listed in Table II the bitter principle composition of four species of *Momordica* (*M. balsamina* L., *M. charantia* L., *M. clematidea* Sond. and *M. foetida* Schum.) and *Raphanocarpus welwitschii* Hook. f. was investigated. Although crude bitter foams were isolated in good yield, none of these foams produced any spots on paper chromatograms with the spray reagents used.

The results in Table II present the maximum number and concentrations of bitter principle found in any sample of a species. The bitter principle composition of certain species may, however, vary considerably, e.g., various species of *Citrullus*, *Cucumis*, *Cucurbita* and *Lagenaria* occur in bitter and in non-bitter forms. Different lines of *Cucurbita pepo* var. *ovifera* contain from one to 8 different cucurbitacins, although always in certain combinations. It appears that the amounts of bitter principles in the Cucurbitaceae is controlled genetically, by environmental factors and by the stage of development of the plant.

Before we continue with a discussion of the distribution of the cucurbitacins in the family, we wish to present a hypothetical scheme of the biogenetic interrelationships of these substances. This is based on a study of the bitter principle associations found in mature plants, the bitter principle changes during the development of plants, and the bitter principle interconversions effected with isolated enzyme systems (18).

E and B Families of Cucurbitacins

The evidence for the existence of two primary cucurbitacins, namely, cucurbitacins E and B is as follows :—

(*a*) Apart from cucurbitacin C, these are the only cucurbitacins which sometimes occur alone in mature plants.

(*b*) Seedling roots of all 21 species investigated contain mainly cucurbitacins E and/or B, even in species which contain as many as eight different cucurbitacins in their mature parts.

TABLE III

Species	Cucurbitacins present in								
	Radicles				Cotyledons				
	B	D	E	I	B	C	D	E	I
Acanthosicyos horrida Welw.	+++	...	...	...	(+++)	...	(++)	...	...
Benincasa hispida (Thunb.) Cogn.	tr	...	...	...	...	...	...	...	...
Bryonia dioica Jacq.	...	...	++	...	...	...	...	++	
Citrullus colocynthis (L.) Schrad.	...	...	++	...	...	...	...	++	...
Citrullus ecirrhosus Cogn.	...	...	++	tr	...	...	...	++	tr
Citrullus vulgaris Schrad., wild	...	...	++	...	...	...	...	++	
Citrullus vulgaris Schrad., water-melon	...	...	++	...	...	...	...	++	...
Cucumis angolensis Hook. f.	++	...	...	...	++	...	tr	...	...
Cucumis anguria Linn.	...	...	...	...	+	...	...	...	...
Cucumis longipes Hook. f.	++	...	...	...	++	...	...	...	...
Cucumis leptodermis Schweick.	++	...	...	...	++	...	...	...	...
Cucumis melo Linn., musk-melon	++	tr	...	...	++	...	tr	tr	...
Cucumis myriocarpus Naud.	++	...	...	...	++	...	...	...	...
Cucumis prophetarum Linn.	+	...	...	...	++	...	tr	...	...
Cucumis sativus Linn., 'Hanzil'	++	...	...	...	++	+	...	...	...
Cucumis sativus Linn., cucumber	++	...	...	...	++	+	...	...	...
Cucurbita maxima Duch., squash	++	tr	+	...	++	...	+	+	...
Cucurbita mixta Pang.	...	...	...	...	(+)	...	...	...	...
Cucurbita pepo Linn., convar. *microcarpina* Greb.	++	...	++	...	++	...	...	tr	...
Cucurbita pepo Linn., pumpkin	tr	...	++	tr	++	...	+	+	...
Lagenaria mascarena Naud.	++	...	...	...	++	...	...	...	...
Lagenaria siceraria (Mol.) Standl.	tr	...	++	tr	tr	...	...	++	tr
Luffa acutangula (Linn.) Roxb.	++	...	++	...	+	...	...	++	...
Luffa cylindrica (Linn.) Roem.	++	...	...	...	...	...	...	...	...

Distributions of the Cucurbitacins

+++	Amount of bitter principle 0·1 per cent or higher ;
++	amount of bitter principle 0·01–0·09 per cent ;
+	amount of bitter principle 0·001–0·009 per cent ;
tr	trace of bitter principle (less than 0·001 per cent)
()	bitter principle present exclusively or mainly as glycoside ;

Reaction I ($E \rightleftharpoons B$)

A reversible enzyme system interrelates the two primary bitter principles. This postulation is supported by :—

(*a*) Cucurbitacins E and B sometimes occur together.

(*b*) A species such as *Lagenaria siceraria* which contains predominantly cucurbitacin B in its mature roots and fruits, contains only E in its radicles and cotyledons.

(*c*) The fruit juice of non-bitter forms of *Lagenaria siceraria* contains enzymes capable of transforming added cucurbitacin E-glycoside in good yield to cucurbitacin B-glycoside. The reverse reaction proceeds in lower yield when cucurbitacin B-glycoside is added to the same plant juice.

The nature of the structural changes brought about is uncertain as a result of our inadequate knowledge of the precise functional differences between cucurbitacins E and B.

Reaction II ($B \rightarrow A$)

The evidence for reaction II in which cucurbitacin B is transformed to cucurbitacin A rests mainly on the following :—

(*a*) Cucurbitacin A is never found in the absence of B.

(*b*) The seedling roots of *Cucumis myriocarpus* contain exclusively cucurbaticin B. The young fruits contain cucurbitacins B and A in a ratio of 2 : 1 whereas in ripe fruits the ratio is 1 : 3.

Cucurbitacins A and B are chemically very closely related. Established functional differences are the absence in A of the α-diketo grouping present in B. Furthermore cucurbitacin A contains an additional hydroxyl group.

Reaction III ($B \rightarrow C$)

Although cucurbitacin C usually occurs alone in mature plants, it is never found in seedling roots. Seedling roots of *Cucumis sativus* contain only cucurbitacin B, cotyledons at a very early stage of germination B with only traces of C whereas fully expanded cotyledons contain only C with no trace of B.

Cucurbitacin C differs from B mainly in the absence of the α-diketo grouping, probably due to reduction of a carbonyl group to a methylene.

Reaction IV ($E \rightarrow I$; $B \rightarrow D$; $C \rightarrow F$)

This reaction has been selected for a more detailed investigation because it is very common in this plant family. Thus an association between cucurbitacins E and I, B and D and between C and F has been observed in approximately 80 per cent of all the species investigated.

The presence of an enzyme capable of transforming cucurbitacins E, B and C to the desacetyl cucurbitacins I, D and F respectively has been demonstrated in the fruit juice of a large number of species. The highest activity so far was found in the fruit juice of the non-bitter Golden Hubbard squash. By a combination of ammonium sulphate precipitation, dialysis and freeze drying, a highly active enzyme preparation was obtained. The purification and properties of this ester hydrolase are being studied by Dr H. M. Schwartz and Miss A. E. van Kerken of the National Chemical Research Laboratory. The reaction with *o*-nitrophenyl-acetate is used as a method of estimation. The liberated *o*-nitrophenol is estimated colorometrically.

Usually this preparation of the deacetylase shows some activity for reaction I ($E \rightleftharpoons B$). This is clearly illustrated by an experiment in which the enzymatic transformations of cucurbitacin E-glycoside was studied relative to time. The reaction was followed on paper chromatograms.

The cucurbitacin I produced was isolated in the crystalline state and found to be identical (m.p. and infra-red spectrum) with a sample isolated from the roots of *Citrullus ecirrhosus*.

Another route to cucurbitacin F apparently proceeds via cucurbitacin D in the leaves and fruits of *Cucumis angolensis*.

Reaction V (D→G and H ; I→J, K and L)

Little is known of this reaction which appears to operate mainly in the roots of plants. The cucurbitacins formed differ from the parent substances mainly in their lack of an α,β-unsaturated keto group. Cucurbitacin G and dihydrocucurbitacin D (produced by catalytic reduction over palladium on calcium carbonate) gave practically identical m.p., mixed m.p. and infra-red spectra, but differed in their paper chromatographic behaviour. Cucurbitacins J, K and L are probably very closely related since they give practically identical infra-red spectra.

The main conclusion emerging from this study of the biogenetic interconversions is that there are only two primary bitter principles, which are chemically very labile, and easily transformed to other related substances by enzyme systems present both in bitter and non-bitter plants. It is therefore not surprising that a knowledge of the bitter principle composition of species appears to be of little value to the taxonomist. However, a few interesting observations have been made. All species of *Cucumis* investigated contain cucurbitacin B and *Citrullus* species only E in their seedling roots. Two species of the same genus can, however, also differ in this respect, e.g., *Cucurbita maxima* and *Cucurbita pepo*.

Since the formation of the cucurbitacins A, C and F is governed by enzyme systems of a relatively limited distribution, these bitter principles are characteristic for only a small number of the species investigated. Thus cucurbitacin A is characteristic of the related *Cucumis myriocarpus*, *C. leptodermis* and *C. hookeri*. Cucurbitacin C has been found only in *Cucumis sativus* (the only Asiatic species of *Cucumis* investigated). *Cucumis angolensis* is characterized by the presence of cucurbitacin F in its leaves.

The distribution of bitter principle glycosides also offers little information of value for the taxonomist. The greatest difference was found between the genera *Citrullus* and *Cucumis*. In the former the bitter principles are mainly present as glycosides, whereas in the latter they always occur free. On the other hand bitter principles occur in *Acanthosicyos horrida* as glycosides in the roots and as the aglycones in the fruit.

Inheritance of Bitterness in Cultivated Cucurbits

An investigation of the inheritance of bitterness is being undertaken at the Pretoria Horticultural Research Station using cultivated varieties of cucurbits. The discovery that the seedlings of most varieties are bitter whether the fruits are bitter or not, indicates that plants with bitter seedlings but non-bitter fruits must possess a mechanism which inactivates the gene for bitterness in the fruits or destroys the cucurbitacins as soon as they are formed. This suppressing mechanism is governed by a single recessive gene in the water-melon variety Hawkesbury, in cucumbers (varieties Early Fortune × Hanzil) and in calabashes (*Lagenaria siceraria*).

The genes governing reactions I and IV are being studied with non-bitter forms of *Cucumis melo* and bitter forms of *Cucurbita pepo*. Several lines have been found which differ greatly in their enzyme activity.

The formation of elaterase appears to depend on the presence of the cucurbitacins. All non-bitter plants in the F_2 and F_3 of bitter × non-bitter *Cucumis sativus* lacked elaterase activity. The bitter forms segregated into enzymatically active and inactive forms showing that there exists a genetic mechanism for elaterase formation which is independent of the gene for fruit bitterness. Genera, such as *Citrullus* and *Cucurbita* generally lack elaterase activity in spite of the presence of bitter principles, apparently because they lack the gene(s) for elaterase formation. Again no non-bitter plants with a high elaterase activity have been found (no induction of enzyme formation).

Acknowledgments

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THE TAXONOMIC SIGNIFICANCE OF PRIMARY AND SECONDARY METABOLITES

By F. Hegnauer

Leiden

The carbohydrates (primary metabolites) accumulated by plants in vegetative organs very often show a relationship to taxonomic position. The accumulation of sucrose and starch is regarded as the 'common pattern' typical for all phyla of green plants. Partial or complete replacement of sucrose and starch by other oligosaccharides and polysaccharides or by cyclitols or sugar alcohols frequently occur. Such replacements are regarded as specializations. One such specialization is often characteristic for a whole taxon. Repetitions in biochemical evolution are however not uncommon (for instance : inuline type of polyfructosanes occur in some taxa of Chlorophyta, Bryophyta, Monocotyledoneae and Dicotyledoneae).

Centrospermae accumulate many types of secondary metabolites. Most typical are 'nitrogenous' anthocyanins, saponins, organic acids and alkaloids. Some relationships suggested by phytochemistry were mentioned.

THE APPLICATION OF IMMUNOLOGICAL METHODS TO *SOLANUM* TAXONOMY

By P. G. H. Gell, Dr J. G. Hawkes & S. T. C. Wright

The differences between tuber-bearing *Solanum* species are often difficult to elucidate by classical taxonomic methods. Cytological and genetical techniques have, however, proved of considerable value in defining potato species and indicating their relationships.

The results obtained from plant immunological methods agree very well with those from the techniques mentioned above. The communication dealt with the relationships of Mexican wild potatoes to each other and to *S. tuberosum*, and showed that immunological analysis can be an important tool in the hands of the modern plant taxonomist.

Discussion

Dr **J. W. Fairbairn** said that the taxonomic problems presented to the pharmacognosist frequently involve distinguishing closely allied species of dried plant material, usually broken and consisting only of parts of the original plant, e.g. leaves, barks, roots, etc. Every tool of the taxonomist is needed and in some instances the biochemical one has proved very useful. Examples of chemical differences involving *phenolic* substances are: the bark of *Cinnamomum cassia* Blume contains no eugenol in the volatile oil, whereas that of *C. zeylanicum* Nees does. Indian Dill (*Anethum sowa* Roxb.) contains the phenolic substance dillapiol which is absent from European Dill (*Anethum graveolens* L.). The glycosides of *Digitalis lanata* Ehrh. differ from those in *Digitalis purpurea* L. in having an extra acetyl group. *Rheum rhaponticum* L. rhizomes can be readily distinguished from those of closely allied species by the presence of rhaponticin. Bitter and sweet almonds (varieties of *Prunus amygdalus* Batsch.) can only be distinguished by the presence of cyanogenetic glycosides in the former. A more striking illustration of this dependence on 'Chemical Taxonomy' is that of the anthelmintic principle santonin which occurs in species of *Artemisia*. Qazilbasch (*J. Pharm. Pharmacol.*, 1951, **3**; 105) states 'There is no reliable botanical feature, on the basis of which it is possible to distinguish santonin-containing Artemisias from the santonin-free' and to overcome this problem he has devised a chemical test which is actually applied in the field to identify the correct species. These are a few examples of chemical differences but the number is increasing as more and more knowledge of the active principles of medicinal plants is obtained.

OBITUARIES

Angus Herdman Booth, F.L.S., died in the Ridge Hospital, Accra, on 16 March 1958 after a brief illness. At that time, although only 30 years old, he had in his 7 years at the University College of Ghana built up a reputation with his knowledge of the West African fauna which indicated a distinguished future and made his premature death doubly tragic. During extensive travels his studies on the systematics, biology and distribution of West African mammals led to a series of papers on the ecology and zoogeography of the West African fauna and also revealed him as an outstanding field naturalist. His qualities as a scientist were best indicated in his collections which are preserved in the University Museum at Achimota and at the British Museum ; those of the primates already having called forth appreciation. Since he was attempting similar studies on West African mammals as a whole, working on Rodents at the time of his death, the loss to science of his abilities must be incalculable. The feeling which Angus Booth had for animals was shown in his work for the small zoo at Achimota which he largely stocked, and whose inmates often only survived as a result of his patient and personal administration.

To one, not a zoologist, who knew him as a friend his zeal and forthrightness called forth great respect as well as affection. From the strength of his personality it was easy to understand the admiration which the African hunter had for him.

He was educated at Christ's Hospital, London, doing National Service in the Royal Marines before entering Emmanuel College, Cambridge in October 1948 to read for the Natural Sciences Tripos. He graduated B.A. and joined the staff of the Department of Zoology, University College of Ghana (then the Gold Coast) in October 1951.

He leaves a wife and two small children. P. B. Tomlinson.

Mrs **Alice Sophia Cooke,** B.Sc., F.L.S. (Mrs A. S. Bacon), **Alice Sophia Smart** was born in London on 1 June, 1890, one of the 3 children of a skilled iron moulder. From school in Stepney she entered the City of London School for Girls in 1906 and after matriculating was awarded in 1909 one of the first two Drapers Company Scholarships in Science for Women to East London College (now Queen Mary College). Here she came under the inspiring leadership of the late Professor Fritsch, F.L.S., and took part as a student in the earlier investigations into the Heath Association on Hindhead Common. She obtained the degree of B.Sc. (Honours) Botany with subsidiary Chemistry in 1912. After a short temporary appointment as science mistress at Swindon and North Wilts Secondary School and Technical Institute, she was appointed assistant lecturer and demonstrator in Biology at Huddersfield Technical College in 1914. Here she was again fortunate in the dynamic leadership of Dr T. W. Woodhead, F.L.S. She hoped in this post to have time for research for a higher degree, but the long hours of teaching imposed by shortage of staff during the 1914-18 war prevented this, although she made time to help Dr. Woodhead in experiments on control of potato blight by spraying.

During this period in Huddersfield the 1914 war brought a great tragedy to her life. Samuel Bacon, a young librarian, had first noticed Alice Smart because of her unusually wide interests as a borrower at the Public Library. They were married in 1916 and after a brief honeymoon he went to France and was killed in action. With characteristic courage and determination she pursued her scientific career. When she left Huddersfield to go to Brighton in 1920 Woodhead wrote :— " Her kindly disposition has endeared her to all and this has had a marked effect on the students."

As Lecturer in Biology (later Head of the Department) for 30 years at Brighton Technical College, Mrs A. S. Bacon was a memorable botanical teacher to many generations of students, mostly for London external B.Sc.General and Special degrees, and for qualifications in Pharmacy. She possessed an unusual gift for clear and logical exposition in lectures, and in practicals she was genially intolerant of second rate work. At all times she was cheerfully on top of her class. With more advanced students she had an instinct for guiding reading in branches where she claimed no specialized knowledge. Her greatest gift was perhaps that she never examined a plant or looked down a microscope without a feeling of keen anticipation which was communicated to her students. Enthusiasm combined with a demand for high standards made her an outstandingly successful teacher. At Brighton, as in earlier years, a heavy teaching load left her no time for her own research, but she inspired an unusually large proportion of students to take up research as their career. Nearly every week-end saw collecting trips in Sussex or even further afield to provide practical classes with an abundant supply of fresh material, sometimes accompanied by parties of students or by her colleague the late Miss Anne Cottis, F.L.S., a keen amateur botanist. Her knowledge of the Sussex flora was unrivalled. During most of this time her father, who had by then retired, kept house for her, first in Moulescombe and later at Hassocks.

In 1950 she retired from the post of Head of the Biology Department at Brighton, and in the same year married her colleague Mr Henry Cooke, with whom she shared many interests, including a keen interest in former students. She died at Hassocks, Sussex, after a short illness on 21 May 1957.

Mrs Cooke was elected a Fellow of the Linnean Society in 1922 and her special botanical interests are reflected in her long association with the British Bryological Society, the British Ecological Society, and the British Mycological Society. She was also a member of the Royal Horticultural Society, the Freshwater Biological Association, the Brighton and Hove Natural History Society, and the Association of Scientific Workers. In earlier years at Brighton she was a keen supporter of the Holiday Fellowship and she travelled widely in Europe during vacations.

By the death of Mrs A. S. Cooke we have lost a warm friend and inspiring teacher who was, as one former student writes, " a remarkably human person, with a singularly kindly personality and a sparkling sense of humour which was never far from the surface ; two attributes which made her a very likeable person indeed ". P. H. GREGORY.

Charles Henry Curtis, M.B.E., F.L.S., V.M.H. who died on 24 March 1958, at the age of 88 had a long career as a horticultural journalist and had an unusually long record of public service both as a Judge at horticultural shows in this country and overseas and as a member of various committees of The Royal Horticultural Society and of numerous specialist flower societies.

He served his apprenticeship in gardening in several private gardens, starting at the age of 14, and then with the famous Chelsea Nursery of James Veitch and Son. Here it is recorded that as a new junior, not yet acquainted with everyone, he once turned the late Sir Harry Veitch, a formidable figure and head of the firm, out of the new plant section of his own greenhouses. However, they apparently got on together afterwards and Curtis wrote an account of the nursery in the R.H.S. Journal for August and September 1948.

Probably no gardeners get such a thorough training to-day. From Veitch's nursery he went to Kew as a student gardener and stayed to take charge of the Orchid department. Orchids remained one of his main interests throughout his life and the biggest and most important book of the many he published was entitled *Orchids, Their Distribution and Cultivation*. He was editor of

The Orchid Review from 1933 until his death. For a short time he was assistant superintendent of The Royal Horticultural Society's Gardens when they were still at Chiswick. He left Chiswick before the turn of the century to become first sub-editor and then editor of *The Gardeners' Magazine* which he served for 25 years until its closing down in 1917. Soon afterwards he joined *The Gardeners' Chronicle* and became editor in 1919, only retiring in 1950 after 31 years.

He served for over 48 years on the Orchid Committee of The Royal Horticultural Society and was its chairman for the last few years and on the Narcissus and Tulip Committee for over 50 years, for 21 of which he acted as its honorary secretary. He was awarded by The Royal Horticultural Society in 1930 The Victoria Medal of Honour, in 1937 the Veitch Memorial Medal in gold and in 1923 The Peter Barr Memorial Cup. He also for long periods played an important part in the control of the National Chrysanthemum Society and of the National Sweet Pea Society.

Curtis also took a great interest in both charitable and municipal affairs, being for 58 years Chairman of the United Horticultural Benefit and Provident Society and also for some years of the Gardeners' Royal Benevolent Institution. He was for some years Mayor of the Borough of Brentford and Chiswick where he lived.

Curtis was active until within a very short time of his death. Horticulturists are notoriously long lived but few can have had a longer record of active service to his chosen field. When he retired from editorship of *The Gardeners' Chronicle* in 1958 he wrote that he had engaged "for more than half a century in an occupation that has never ceased to be enthrallingly interesting, almost entertainingly varied and always congenial."

PATRICK M. SYNGE.

Cecil Prescott Hurst, who died in 1956 was an enthusiastic student of Natural History, particularly of Field Botany. He spent most of his life in the remote country places that he loved so well, and was not therefore so widely known amongst his professional colleagues as he deserved to be. Although I knew him well from the early 1920's until about 1930, this period represents no more than a small fraction of his active life, but, as he seems to have outlived most of those who were familiar with his botanical work, it has fallen to my lot to place on record such facts about him as I can remember. As a young man Hurst lived in the Isle of Wight and was a keen lover of nature from an early age. Unfortunately he met with an accident whilst botanizing on the island which made walking difficult for him for the remainder of his life. Hurst was a bachelor, and, when I knew him, he lived with his two sisters at Ivy House, Great Bedwyn, Wilts, and he then enjoyed a high local reputation as a field naturalist. Indeed Ivy House became the Mecca for all local botanists, and many interesting and lively discussions must have taken place within its walls. Hurst was an active member of the Wiltshire Archaeological and Natural History Society, a Society which published a number of his articles on the flowering plants, rust fungi, and other groups of plants in the Bedwyn district. Other notes which he made on flowering plants have been embodied in *Reports of the Marlborough College Natural History Society*. It is good to know that some of Hurst's many records of the occurrence of flowering plants in the Bedwyn area have been taken up by Donald Grose in his recently published book *The Flora of Wiltshire*. He corresponded actively with W. B. Grove, Claridge Druce, and other well known botanists of that period. He was also well known to the biological members of the staff at Marlborough College in those days, particularly to L. G. Peirson and A. G. Lowndes, and, through them, Hurst probably played a more important part than is generally realized in arousing and stimulating an interest in Natural History amongst the small band of boys at Marlborough who were then studying biology with more than average enthusiasm. I have most happy recollections of the part he played in developing my own interest in botany, and I kept in touch with him until 1930 when he moved from Bedwyn and went to live near Saltash.

Hurst was, by nature, a shy man, and he made a picturesque figure when working in the field for he was always similarly attired in all weathers and seasons. He was seldom to be seen without an overcoat, and he always carried an umbrella and a newspaper. The newspaper served two purposes, for he read it whilst waiting for the infrequent local trains by which he travelled, and it was subsequently used for wrapping up his specimens. His knowledge of the local natural history always appeared to be unlimited, and his enthusiasm on finding an interesting specimen was almost overwhelming. Hurst could never bring himself to master the art of using a microscope, and this was a great weakness when he was dealing with rust fungi and other microscopical organisms. Nevertheless he was a student of nature in the very best sense of the term, and he undoubtedly had a much closer knowledge of the plant life in the districts in which he lived than is true of many present-day botanists.

C. R. METCALFE.

Dr **Wilfred Rushton** retired from St Thomas's Hospital Medical School in 1952 but he continued with his advisory work, so when he died on 9 July 1957 while attending a meeting, in Cambridge, of the London Angler's Association and the Great Ouse River Board, he died as he had always wished, in harness. To those of us who knew him, his death was no surprise, as he had been in failing health for some time. He was born in Todmorden on the borders of Lancashire and Yorkshire, in 1882. After spending some years in a weaving mill he determined that this was not to be his life's work. He studied in the evenings, his diligence and determination being ultimately rewarded when he won an entrance scholarship to the Royal College of Science, London in 1907. It was this scholarship which started him on his biological career.

In 1910 he qualified A.R.C.S., having specialized in Plant Physiology, and was awarded a research grant which enabled him to continue at the Royal College of Science for another year, where he carried out research work under Sir J. B. Farmer, Professor of Botany. It was in 1911 that he first became associated with Medical Schools when he was appointed Demonstrator in Biology at St Mary's Hospital Medical School . This was not a full time appointment, so in 1912 he took a similar appointment at St Thomas's Hospital Medical School. This work was interrupted during the First World War when he was engaged on biological war work of national importance.

On his return from war work he was appointed (1919) head of the Biological Department at St Thomas's and he gave up his appointment at St Mary's. In spite of the fact that he was still only part time he made St Thomas's his centre and it was under his supervision and guidance that a useful collection of teaching material was built up. It was at this time that he started his research work on freshwater biology. He was a pioneer in this type of research work and soon became a recognized authority on the ecology of reservoirs, pollution of rivers and diseases of fish. His first connection with reservoirs was in 1922 when he was called in as a consultant to the Jersey Waterworks. Later he acted as consultant to the Metropolitan Water Board, the South Essex Water Board and Staffordshire Water Board, to mention only a few. He was always very proud of the fact that he was called in to advise on biological matters when the present Abberton Reservoir, of the South Essex Water Board, was a stream running down the valley, and continued as advisor for this reservoir until his death. His monthly visits to Abberton to sample and check the flora and fauna of the reservoir were always a great source of interest and enjoyment to him. He also acted as consultant to such bodies as the Thames Conservancy, Salmon and Trout Association etc. In recognition of his contribution to our knowledge of freshwater biology, he was awarded the D.Sc. degree of the University of Illinois. Prior to his death he was engaged in writing a paper on 'Some of the diseases of freshwater fish' which, when printed, (we hope in the near future) will mark the climax to half a century of biological work.

Short in stature and lightly built, Rushton will be remembered for his boundless energy, drive and insatiable thirst for knowledge.

He is survived by his wife, daughter and son to whom we extend our sincere sympathy. A. G. HAMILTON.

By the death of Mrs **Menie Watt** on 13 December, 1957—fortunately after a short, painless illness—Edinburgh lost one of its most elegant figures, the Royal Botanic Garden a most staunch supporter, and the writer a personal friend.

She was born in Glasgow on 2 April 1871, the elder daughter of the Rev. W. C. E. Jamieson and Jessie Archibald. Later the family moved to Edinburgh and at the time of his death Jamieson was Minister of the famous Tron Church. In 1899 Miss Jamieson married a distinguished Edinburgh lawyer, James Watt, W.S., who was later to become a Fellow of the Faculty of Actuaries and to receive the degree of Doctor of Laws from the University of Edinburgh. Thereafter she was to spend the rest of her life in the Edinburgh she greatly loved, at first attending to the needs of her five young sons and one daughter, and afterwards devoting herself to her husband in whose work she was of considerable assistance.

Her mother was of farming stock and no doubt it was her uncles, John, James and Adam Archibald, who farmed Overshields, Stow, Midlothian, for many years, who stimulated her interest in plants. Overshields was well stocked with an unusually wide range of botanical and natural history books, and Uncle John apparently was a very knowledgeable botanist. From him and from her own observations she learned much concerning wild plants and especially of the flora of the Lothians.

But it was in garden plants and in the layout and planning of a garden wherein lay her greatest interests and from which she drew most satisfaction. She had a remarkably keen eye for a good garden plant and instinctively knew where to place it in relation to others as well as its cultural requirements. She was, in fact, a considerable landscape artist and the extensive garden at Craiglockart House gave her scope for her ideas. Joyously she moved through various phases, rock gardens, rhododendrons, roses, herbaceous borders, fuchsias, bulbs, and possibly gained the greatest satisfaction whenever the flowers of her Aspidistras almost literally covered the soil in their pots. The Aspidistra she always claimed to be one of the most beautiful as well as the most despised and neglected of plants. And certainly as one saw them in Craiglockart House there was very little amiss with them. But then The House always was lovely with flowers and inevitably so for the Mistress was one of the first in this grey city to practice the art of floral and table decoration. Her ideas on this subject, which is now of universal interest, she expressed in her only book, charmingly written, "Flowers in the Home".

As she grew older, and a little more frail, she did not lose interest in her plants and continued to acquire, and to read, gardening books and nurserymen's catalogues, as well as the Journal and Proceedings of this Society of which she became a Fellow in 1936. Her practical experience, however, had perforce to be limited to what the small house and garden, into which she moved shortly after her husband's death in 1945, could accommodate. Any desires she had for gardening on a grander scale were satisfied by her taxi-visits to the Royal Botanic Garden, and by the National Trust for Scotland's Garden Cruises.

On the evening of 14 November, 1957, she attended a meeting of the Botanical Society of Edinburgh to hear an address I gave on the History of the Discovery of the Scottish Flora. Then, she told my wife that she could not remember when she began to send cards to her friends at Christmas time but that she had decided to discontinue the practice this year. She died a month later.

H. R. Fletcher.

John Christopher Willis was born in Birkenhead, 20 February, 1868. The Willis family had lived in the neighbourhood of Liverpool for some generations, had intermarried with the Swainsons and his paternal grandmother was a daughter of John Timothy Swainson, a founder-fellow of the Linnean Society, and sister of the eminent biologist William Swainson whose career began in the Customs Office of Liverpool. Richard Charles Willis, his father, was a restless young man who wandered into many parts of the world, returned home, married (1867), and entered business, including the establishment of a boat-building yard in Hoylake ; but, tiring of his surroundings, he uprooted his family (1886) and took them to a farm near Seattle which was then almost the most remote spot in the United States, leaving John whose education was too far advanced to be broken. Thus John became very early more or less his own master. He had been educated at the Birkenhead School and was attending at University College, Liverpool, a rather curious assortment of classes—mathematics with physics and latin with german. He was uncertain of his future, but taking bearings by sitting for examination at several educational centres ; in the very month of his parents' departure he obtained a Clothworkers Society's scholarship tenable for three years at Cambridge and entered the University as a non-collegiate student. He read for the Natural Sciences Tripos and took the first part with a First class at the end of his second year. Illness prevented him from taking the second part. Caius College chose him to be their Frank Smart Student (1890). In 1892 the University Board of Studies in Biology and Geology recognized him as a Lecturer. The College prolonged his Studentship for a fourth year.

His migration to Caius brought me into his company, and we commenced to take exercise together during term and, later, holidays together.

His first research was on a suggestion from Sir Francis Darwin that he should attempt to track down the cause of gynodioecism in the Labiatae. Three short papers resulted without the discovery of a cause capable of isolation. Flower-biology in other directions intrigued him and he wrote several papers on devices in flowers leading to pollination. Our joint walks from Cambridge led to recording the plants which find their way into the tops of pollard willows and taking evidence on how they do it : our joint holidays allowed us to take notes on insect-visitors to flowers. We were less interested in what the insects were than in their sufficiency, but found means of identifying the insects. Finally, taking Glen Clova, in the Grampians, for our workshop, we set out to count the visitors observed, omitting no species, neither of plants nor visitors, and prepared ourselves by exhausting the literature for comparisons of any one alpine plant at Clova with it in the Arctic, the Alps and elsewhere. We knew of plenty of claims that what was cross-pollinated in one place might be self-fertilized in another in obedience to Natural Selection. Our extensive data were ultimately published in the *Annals of Botany* when, after six years, neither of us was able to continue the visits to Glen Clova. We had made a thorough survey of the flora, with phaenological records which were printed to show that there was a sudden bursting into flower in the spring and an intensification of flowering of bee-flowers towards autumn. Raunkiaer made use of these.

Willis, after holding the Frank Smart Studentship for four years was appointed (1894) Senior Assistant to Professor F. O. Bower in the Botany School of the University of Glasgow and Lecturer at the Queen Margaret College.

While still an undergraduate in Cambridge he had devised his own way of assimilating taxonomic facts; it consisted of summarizing from the books with which he worked what they taught; and the scope was determined by the families and genera named in the text-books and the plants he knew in the field and particularly those on display in the University Botanic Garden. When he began to teach, it occurred to him that what had served him would serve another passing through his course, and he began to order and extend his summaries, thus was formed his *Dictionary of the Flowering Plants and Ferns*. He had it fairly advanced when the vacation of Easter, 1896, gave him the chance of working on it at Kew. Bower, in saying goodbye to him, bade him call at Kew on the Director, Sir William Thiselton-Dyer. Dyer and Bower had been in correspondence regarding a successor to Henry Trimen as Director of the Botanic Garden at Peradeniya, Ceylon; and, half joking, Bower had told Dyer that Willis would make a particularly excellent colonial official because he liked statistics so much. Willis paid the call and was overjoyed at the offer of nomination for the post at Peradeniya. Then followed a tremendous effort to clear the *Dictionary* from his desk before sailing, which was not quite successful, but nearly so. He worked at it through the voyage; and the Press had it out in two parts, one on either side of Christmas, 1896. The proof-reading had been entrusted to Miss Minnie Baldwin, afterwards Mrs Willis, daughter of Thomas Baldwin, the senior schoolmaster and Clerk to the Barnsley (Yorkshire) Education Committee. Miss Baldwin was at the time teaching in the Westfield College, Hampstead. Willis had discovered a real need; and the 8th edition of the *Dictionary* is now in use.

There was much more in the choice of Willis to succeed Trimen than appears on the surface. Scientific Botany had acquired a new front and the sending out of him was for the bringing of Ceylon into line. Ceylon's official gardens—Colombo, 1810–13; Kalutara, down the coast, 1813–21; Peradeniya, 1821 forward—were but plant-introduction centres at first, and therefore under the charge of horticulturists: in 1844 with the appointment of George Gardner, Peradeniya passed into the charge of the first official botanist that the island had with the intention that he should give service beyond what the horticulturists could give, namely, should determine the species of plants in the island. Gardner, followed by Thwaites, followed by Trimen, had done this, and Trimen's *Flora* had consummated the work of the three when Willis was chosen to spread the new outlook.

A sign of the need had been the temporary employment (1882–85) of Marshall Ward for a study of the Coffee-leaf disease in hope of being able to suppress it. Though large quantities of specimens of fungi had been sent to Berkeley to be named, that was not enough; means were desirable for study in life of all the lower plants and for a fuller knowledge of the higher—in brief for whatever is achieved by the microscope and a laboratory. Just after Marshall Ward's departure visiting botanists began to appear in Ceylon in appreciable numbers, and a small room became a work-room that they could use. It was obviously profitable to encourage them. They and Willis were of the same school and could march together.

Willis was the instrument of great changes, some certainly not anticipated by those who chose him. When he arrived the superior staff consisted of himself and two horticulturists, one at Peradeniya and one at the branch garden of Hakgala: when he left 11 were in the place of the three; and visiting botanists had been numerous. There was great activity. In Ceylon when it had been impossible any longer to grow coffee, the planters had turned to cinchona and cardamons ; now tea was making the island very prosperous. Rubber was experimental in the hope that it would be remunerative. Part of the increase of staff was for new crops ; part for protection against pests ; part for taxonomic study of lower plants ; two chemists and an entomologist were among the number and there was an educational officer to spread familiarity with useful plants through school gardens. At 1900 the estate of Gangaruwa, adjoining Peradeniya, was acquired for technical training of intelligent young men with the intention of reaching the peasant thereby. In 1900 also a new laboratory was provided. Undeniably the whole amounted to a Department of Agriculture, as indeed Willis called it ; and the Colonial office wrote "the time has come when the present somewhat misleading title should be changed to that of Deparment of Agriculture". That this was so was his undoing. A scheme was devised : a very high-standing and experienced professional agriculturist was to be sought and appointed Director of Agriculture, with as his first Assistant one who could spread new ways through the vernacular languages of the island ; Willis was to be shorn of his staff except enough only to manage Peradeniya and Hakgala ; and the new Director of Agriculture was to be in a position to demand services from him. The whole was so humiliating that he resigned—not merely personally humiliating, but humiliating to the Gardens in a way to make the Assistant Director refuse the succession when it was offered to him. Protests appeared in Ceylon and London ; one in *The Times* of 27 May, 1911, was over very eminent signatures ; and the Colonial Office admitted that his work for the planting community had been excellent. His reputation as an organizer had led to him being deputed in 1904 to Malaya to advise ; and he was asked to give a course of lectures, being on leave in the United States, at Harvard University (1909). As soon as it was known that he was breaking his connection with Ceylon he was offered the position of Director of the Botanic Garden at Rio de Janeiro for three years during which he was to reorganize it. So to Brazil he went in December, 1911.

After serving his three years there he returned to Cambridge where he taught—along with geographical Botany—Portuguese which he had mastered. In Ceylon from 1905 to 1911 he had edited *The Tropical Agriculturist*. From Cambridge he began (1923) to edit the journal of the British Cotton-growing Corporation and did so until 1939 ; but in 1931 he had moved, for the sake of the health of his wife, to Montreux, on the Lake of Geneva, where (1931) Mrs Willis died. He remained at Montreux until his death, 21 March, 1958.

I pass to the writing that he did after leaving Britain in 1896. Much of it was agricultural ; and of that it is enough to say that it was accurate and helpful ; there was very much botanical. It is necessary to preface the record by mentioning a serious accident which he had in 1907, because he attributed his choice in work to the accident. He was out one day in the mountainous centre of Ceylon and did not return when expected ; those who went to seek him, found him unconscious by a bicycle from which he certainly had fallen. He had sustained a concussion which cost him the use of one eye and in after-life he maintained that the injury had sent him in-doors to seek the satisfaction that he got out of work.

In 1896 on his arrival in Peradeniya he, so to speak, read himself in by familiarizing himself with all that the Garden displayed, writing a new guide book (1898). Then he compiled a catalogue of the Flowering plants and Ferns of Ceylon from the work of his predecessors.

In the years 1899-1901 Professor Stanley Gardiner was collecting through the islands of the Indian Ocean, and took his Maldive plants to Peradeniya for determination. Trimen had written on the Maldive flora and this was natural. Gardiner and Willis collaborated, and Willis added an account of the flora of Minikoi from material which had come to him. By the time that the two papers were ready he had been able to found his *Annals of the Royal Botanic Gardens, Peradeniya*, and the papers were printed in it. Gardiner was again in the Indian Ocean in 1905 on the ' Skylark ' expedition ; and he and Willis again worked together, the islands this time being the Chagos archipelago. The Maldives were found much influenced by Man ; other agents had carried migrant plants to them in this order—birds, currents, winds. Winds had carried Cryptogams chiefly. The Laccadives had been influenced conspicuously by birds. The floras were called " a miscellaneous assortment . . . that might have come from any palaeotropic country." The next researches had a greater interest.

The river Mahaweliganga in its nearly complete circuit of the Peradeniya Garden has rapids on the rocks of which grow Podostemaceae. Willis monographed the family, starting his work in Ceylon, making two journeys in India to see them in the Western Ghats and the Khasia Hills and later he was to study those of Brazil. The Podostemaceae altered his views on Natural Selection. The last of three papers on them (*Proc. Roy. Soc.* B. 87 : 1914) is a review in which he emphatically stated that beyond an invariable adaptation to growth in rapidly running water there was nothing in them of an origin that is attributable to Natural Selection ; yet they exhibit great morphological differentiation. The family, he claimed, had mutated into all this, which view, he stated, had come to him in 1904 ; and he had published it first in 1907.

He had proceeded from compiling his catalogue of the flora of Ceylon to an analysis from the phytogeographical standpoint, paying attention particularly to the endemic species. He now claimed that these endemics, like the Podostemaceae, had mutated where they were to be found, inheriting from their parents a suitability to it, but not there by reason of greater suitability such as under Natural Selection would cause them to take possession and, oust, according to views commonly held, the less closely adapted parents. The reader will realize that he was bringing the endemics into line with the Podostemaceae. Discrediting Natural Selection as shaping these endemics, he claimed that their area indicated their age from creation by mutation ; and the endemics that he had particularly studied he classed from their very restricted area as young species. He was careful to qualify an extended claim that most endemics are such, by ' on the average '. The paper in which the claim was made was of 1915 (*Phil. Trans. Roy. Soc.* B. 206) ; the third of the papers on Podostemaceae was of 1914. In the paper of 1915 he made a claim, ex cathedra, that mutations could be of any dimension, throwing larger units than species, perhaps subgenera and possibly even genera.

Edmund Sinnott and Irving W. Bailey had been using Trimen's *Flora of Ceylon* for showing that herbs produce new species more rapidly than trees. Of the critics who came forward it is enough to mention Sinnott who had made himself familiar enough with Willis's substratum. He confined himself almost entirely to the claim ' Age and Area ', admitted Age as one factor in determining Area, but pointed to release from fresh mutability, freedom from hybridization, readiness with multiplication, escape from heavy competition or from alteration of environment as factors mixed into a complex beyond such a simple solution as ' Age and Area ' offered. Furthermmore he gave as his belief that relicts exist in the World in an abundance that Willis did not admit ; and that the pressure of Natural Selection could be very real. Willis's reaction to criticism was a considerable series of papers, one of which was entitled *Further evidence on Age and Area* and all might have been so entitled, and then a book (1922) with *Age and Area* as its title. He had turned to New Zealand.

Willis's paper on the Podostemaceae had stimulated Dr H. B. Guppy into writing on mutation (*Journ. Linn. Soc. Bot.* 44, 1919). The two were near together in thinking ; and neither saw in mutations as present conditions show them, time enough for the building up of the systematic tree. Guppy suggested, claiming it unreasonable to judge the past by the present, that mutating had been much more rapid in the past than it is now: Willis suggested a great size for mutations, a new genus, for instance, at a single change. He suggested that it might be multiple. It is not difficult to imagine a concatenation appearing to be a single mutation if it be built up of a succession of similar mutations which Natural Selection could push into the same direction. He postulated his big mutations as geologically remote and as the beginnings of new families. There seems little repugnant to a belief in evolution changing pace with the Earth's changes—a belief that is a little helpful to his theory; but it leaves his postulate no more than a postulate. He had brought up a big problem that was to occupy him for the rest of his life.

Natural Selection provided for the ousting of the parents by the children being more suited to their environment. Willis's big mutations could let both live by carrying the new species beyond a recall by back-crossing.

Early in his work, he had observed that a relatively consistent curve—a hollow curve folding on itself at a more or less consistent position above zero—was given on plotting the genera of a family by size in species. The consistency made him hope that he was on the track of a law of mutation. He assumed that the abstractions—genera and species—represent a reality and built on them. Was he justified? Sir David Prain, addressing the British Association at Winnipeg, had called the genus a thing of dignity because of its relative stability—could one say representing a real concord with Nature? Parenthetically it is mischief to split a genus on the plea that it is inconveniently large, but it has been done. Taking his risks Willis put an immense amount of work into a search for that law. Claiming the size of a genus to declare its age, he called the *largest* of a family the leader assuming it the *oldest*. It would seem that he was faced in this by many imponderables.

He deduced from the uniformity of the curve and its apparent universality that it exposed a common character, that could not be Natural Selection, for a curve resulting from Natural Selection should be as variable as are the agencies in Natural Selection. The alternative was mutation as common to all.

Having reached the conclusion that large mutations occurred in remote geological times, he was led to postulate that the old families would arise by the largest mutations and that lesser mutations divided them up. A large mutation could remove the daughter species from the possibility of re-incorporation in the parent by back-crossing; and the more divergent the more effectively.

His book entitled *Age and Area* (1922) was followed by *The Course of Evolution* in 1940 and this by *The birth and Spread of Plants* in 1949—this last a volume of the Swiss journal *Boissiera*. In the introduction to it he refers to the vast accumulation of statistics which he was leaving in the hope that another would take up his subject. The book ends with 22 pages of aphorisms which in an interesting way expose his philosophy. He was in the habit of writing down a thought as it came to him and slept with a memorandum block at his bed-head. Many of the aphorisms would be taken from the notes that he had made; when sorted later the thought which led up to them had been left behind and he called them sub-consciously realized.

Of his three daughters one survives him; the second Margaret Anderson was a Fellow of Girton and University Lecturer in Geography.

The University of Cambridge gave him the degree of Sc.D. in 1905 and the Harvard University the same degree (1909). He was elected to the Royal Society in 1919 and to an honorary membership of the Deutsche Botanische Gesellschaft. The Linnean Society awarded to him in 1958 one of their Darwin-Wallace Silver Medals; but his death came before it could be presented.*

* Accepted by grandaughter on 15 July 1958.

Age and Area, stripped of a claim that relicts are few, is ready for limited application in Phytogeography, as he applied it in suggesting that there had been two land-bridges into New Zealand. The end of disputing about the size and frequency of mutations is not in sight; nor whether it is well to call nascent mutations divergent. I. H. Burkill.

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